DEVELOPMENT OF INFAUNAL POPULATIONS AND BELOW-GROUND ORGANIC MATTER FROM THREE CREATED *SPARTINA ALTERNIFLORA* MARSHES IN GALVESTON BAY, TEXAS

A Thesis

by

ALISHA RENEE GOLDBERG

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 1996

Major Subject: Wildlife and Fisheries Sciences

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December 1996

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Development of Infaunal Populations and Below-Ground Organic Matter From Three Created *Spartina alterniflora* Marshes in Galveston Bay, Texas. (December 1996)

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High rates of wetland loss in the northern Gulf of Mexico have stimulated efforts to create marshes on dredged material. These marshes may not function similarly to their natural counterparts in supporting infaunal populations used as food by estuarine animals. Newly created marshes often have relatively low levels of organic matter in the sediments and low infaunal abundance. However, organic matter and infaunal populations in created marshes may develop over time. To examine the relationships between infaunal abundance and sediment parameters, two created marshes (ages 5 and 9 years) were compared with a newly created marsh in the same location. Over a two-year period, core samples were taken quarterly to measure infaunal density, live root and detritus biomass, and sediment organic content and grain size, at different elevations in each of the

marshes. Samples were collected at and between culms of *Spartina alterniflora*. The vertical distribution of the infauna was also examined. Overall infaunal densities and species richness in the youngest marsh were comparable to those in the other marshes within the first year. However, the newest marsh was dominated by the subsurface deposit feeding polychaete, *Capitella capitata*, while the two older marshes were dominated by the surface deposit feeding polychaete, *Streblospio benedicti*. In general, low elevation was correlated with high infaunal abundances, more animals were collected in cores at culms of *Spartina alterniflora*, and most of the infauna were found in the upper 2.5 cm of sediment. There was evidence of accumulation of organic matter over the two-year study period, and organic matter levels were lowest in the newest marsh. There was no general relationship between concentrations of sediment organic matter and detritus and infaunal abundance. However, there was a positive relationship between infaunal abundance and the amount of live roots and rhizomes present, and this relationship appeared strongest during spring and summer. The results of this study suggest that factors other than organic matter concentrations control infaunal populations.

ACKNOWLEDGEMENTS

I would like to express my appreciation to the members of my committee, Dr. R. Douglas Slack, Dr. Thomas Minello and Dr. Donald Harper for their input and instruction, and for being so generous with their time. Special thanks to Dr. Teresa McTigue, Shannon Whaley and Amy Innes for their assistance and insight. A million thanks to my mother, Judith Goldberg, and my husband, Benjamin Higgins, for their support and encouragement. This work was funded by the Restoration Center and the Southeast Fisheries Science Center of the National Marine Fisheries Service and was completed using the facilities of the National Marine Fisheries Service Laboratory in Galveston Texas. I would also like to acknowledge the staff of the Galveston lab for their assistance with the collection and processing of samples.

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INTRODUCTION

Benthic infaunal populations in salt marshes of the northern Gulf of Mexico are important sources of food for estuarine nekton that forage in this intertidal habitat (Weisberg and Lotrich 1982; Kneib 1985; Rozas and LaSalle 1990; Minello and Zimmerman 1991). Therefore, extensive losses of salt marsh occurring in the region may have serious negative impacts on estuarine food webs. Creation of new salt marshes through the planting of *Spartina alterniflora* on dredged material has been promoted as a possible means of restoring a portion of this lost habitat (Broome et al. 1988; Webb et al. 1978; Woodhouse et al. 1972). Development of above-ground biomass in created *Spartina* marshes is generally rapid (Webb at al. 1978; Race and Christie 1982; Seneca et al. 1985; Webb and Newling 1985; Broome et al. 1986). However, above-ground plant characteristics, such as density and biomass, are not correlated with animal abundances in created marshes (Cammen 1976a; Moy and Levin 1991; Minello and Zimmerman 1992). Benthic infaunal populations in created marshes do not appear equivalent to those in natural marshes (Cammen 1976 a, b;

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Moy and Levin 1991; Sacco et al. 1994). Often, an assumption is made that sediments and infaunal populations in created salt marshes will develop over time and eventually reach levels in natural marshes. Estimates for completion of this process, however, have been as long as 30 years (Craft et al. 1988; LaSalle et al. 1991). Most studies on created marshes have been conducted along the Atlantic coast, and there is some evidence that infaunal populations develop more rapidly in Gulf coast marshes (Minello and Zimmerman 1992). These estimates of development time are generally made through comparisons of different-aged marshes in different locations. Such comparisons are complicated by other differences among marshes, perhaps unrelated to age, that affect infaunal populations (Sacco et al. 1994).

Biological interactions, such as adult-recruit interactions (Kent and Day 1983), competition (Peterson 1977; Wiens 1977; DeWitt 1987; Kristensen 1988; Taghon 1992), larval settlement (Rodriguez et al. 1993), and predation (Woodin 1974; Bell and Coull 1978; Virnstein 1979; Kent and Day 1983; Kneib 1992; Service et al. 1992) are known to affect infaunal populations in natural marshes. Environmental factors, such as disturbance

(Flint and Younk 1983), salinity (Flint and Younk 1983; Dauer et al. 1987; Jones et al. 1990), dissolved oxygen (Dauer et al. 1992), photoperiod (Chu and Levin 1989), hydroperiod (Kneib 1982; Kneib 1992; Rozas 1995), and temperature (Chu and Levin 1989) have also been determined to influence infaunal populations. In addition, characteristics of the substrate, such as sediment grain size, organic content and below-ground plant biomass have also been shown to affect the abundance and distribution of infauna (Whitlach 1980; Osenga and Coull 1983; Butman and Grassle 1992; Minello and Zimmerman 1992; Jaramillo et al. 1993; Long and Poiner 1994; Sarda et al. 1995).

Relatively little research has been conducted in created marshes, but some relationships have been observed between infauna and sediment parameters, such as sediment organic content and below-ground plant biomass. Below-ground biomass, sediment organic content, and infaunal densities are often lower in created marshes compared with natural marshes (Cammen 1976a, b; Webb et al. 1978; Lindau and Hossner 1981; Langis et al. 1991; Moy & Levin 1991). Minello and Zimmerman (1992) found a strong correlation between sediment macroorganic matter and infaunal density during spring in created marshes

between 2 and 5 years of age. The development of below-ground organic matter may affect the development of infaunal populations in a variety of ways. Moy & Levin (1991) suggested that the abundance of deposit-feeding organisms may increase with increased detrital food associated with below-ground biomass. Roots and rhizomes may provide structure within the sediment that may be important in reducing competition within the infauna or reducing foraging efficiency of predators on infauna. Also, live *Spartina* roots produce micro-oxygenated zones (Teal & Kanwisher 1966; Armstrong 1979), and these zones could provide additional inhabitable space within anoxic marsh sediments (Osenga & Coull 1983; LaSalle et al. 1991).

The objectives of this study were: 1) To examine the development rate of infaunal populations in created salt marshes of Galveston Bay, Texas; 2) to examine some potential factors regulating these populations; and 3) to examine the vertical distribution of the infauna within the sediment. In an attempt to eliminate many of the location-related differences among marshes, I selected three created salt marshes on Pelican Spit, all located within a 60-hectare area. One marsh was newly created at the time sampling was initiated in 1992, and the others

were 5 and 9 years old, respectively. I measured infaunal densities quarterly for a two-year period at two elevations in each marsh, and collected samples both with *Spartina* culms and between plants (no culms). Infaunal abundances in the marshes were compared with sediment grain size and biomass of live *Spartina* roots, detritus, and sediment organic matter. I also compared infauna and macroorganic matter levels from the two older marshes at Pelican Spit before and after establishment of the newest marsh, and compared data from the two older marshes to data obtained from a nearby natural marsh as part of a previous study.

METHODS

Study Area

The study area included three created salt marshes on Pelican Spit, a small, undeveloped island in Galveston Bay, Texas (Fig. 1). All three marshes had sediments of dredged material, were dominated by *Spartina alterniflora*, and were located within an area of approximately 60 hectares. The oldest marsh was established naturally on dredged material deposited in 1983 (83Marsh). In 1987, newly-deposited dredged material was planted with *Spartina* on 1-m centers to create the 87Marsh. Dredged material was again deposited on the spit in January 1992, and planting was completed in early July. As a result, the 92Marsh was less than one month old when sampling was initiated.

Within each marsh, I established two transects parallel to the marsh-open water interface. Edge transects were located approximately 1 m in from the open water at the same elevation in each marsh. Inner transects were located further into each marsh at an elevation 20 cm higher. Marsh slopes varied; the inner transect was approximately 2-3 m from the marsh edge in the 83Marsh, 4-6 m in the 87Marsh, and approximately 75 m from the edge in the 92Marsh. I installed permanent

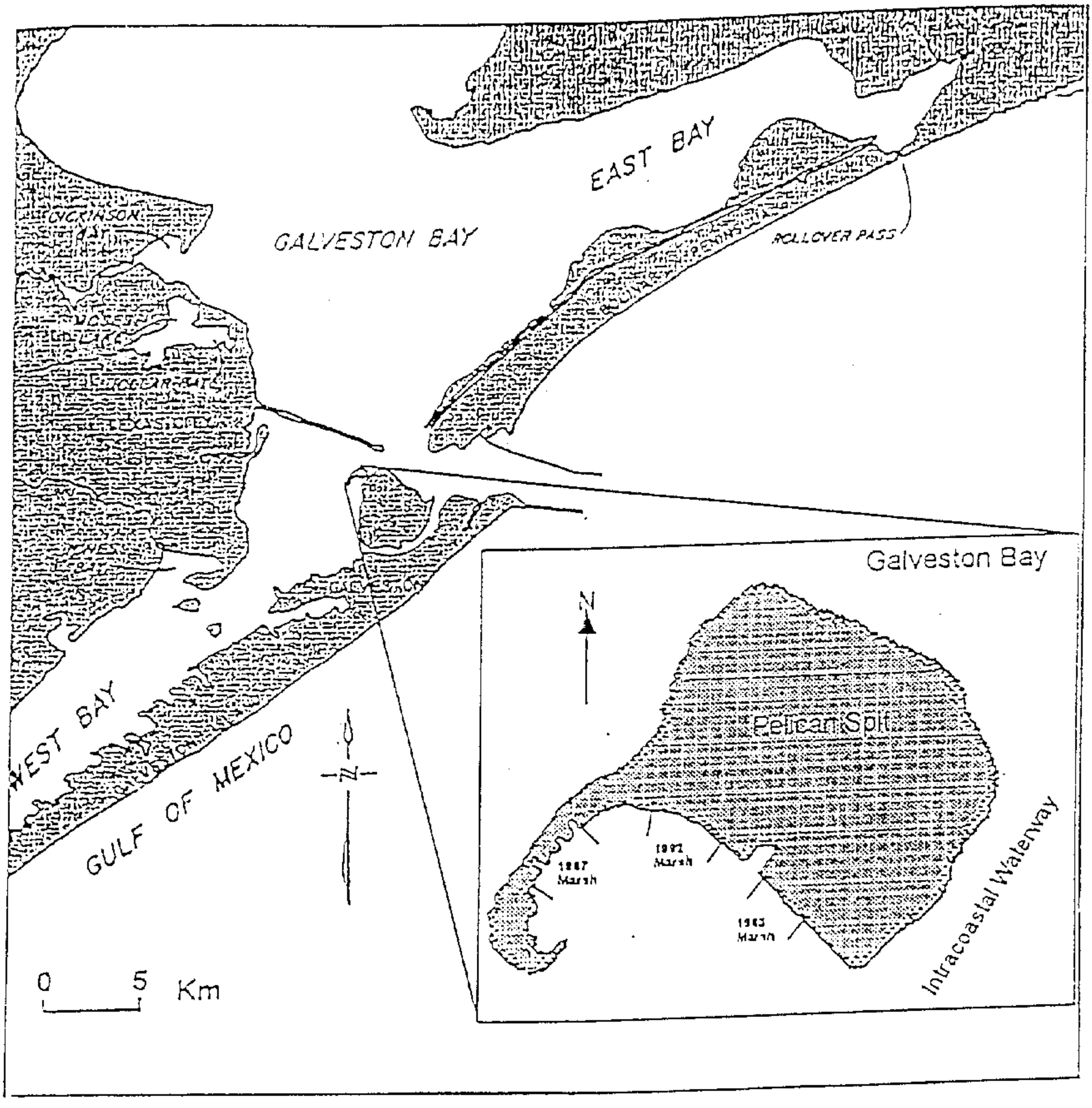


Fig. 1. Location of the three created *Spartina alterniflora* marshes on Pelican Spit in Galveston Bay, Texas.

staff gauges near the marshes and used water levels to identify transect locations during each sampling period. When I selected sampling areas in July 1992, it was apparent that the placement of dredged material for the 92Marsh resulted in some new sediment deposition on portions of the 83Marsh and 87Marsh. Therefore, I restricted sampling in these marshes to areas farthest away from the 92Marsh; these areas did not appear to be impacted. Transect lengths were 60 m in the 83Marsh, 53 m in the 87Marsh, and 165 m in the 92Marsh.

Sample Collection and Processing

I collected samples quarterly for two years, beginning in July of 1992; sampling dates were July 27-29, 1992; October 1-7, 1992; February 24 - March 2, 1993; May 4-5, 1993; July 28-30, 1993; September 28-30, 1993; February 25, 1994; and May 16-20, 1994. During each of these eight sampling periods, I took eight randomly-located sediment samples along each transect, four samples between *Spartina alterniflora* plants (no stems) and four that included the living *Spartina* plants (stems). Although samples that included culms of *Spartina* were designated as samples with stems, the actual stems were cut off at the mudline and removed

before the sample was taken. All samples were collected when tidal water covered the marsh surface. At each sampling site, a 10-cm diameter corer (78.5 cm^2 area) was pushed into the sediment; and a drain spade was used to dig underneath the corer, cut through the root mass, and help lift the core. I divided the upper 5 cm of each core into two 2.5-cm thick sections and processed each section separately to examine the vertical distribution of the infauna. Each section was rinsed in a 0.5-mm sieve, and material retained on the sieve was preserved in 10% formalin with rose bengal stain. I also collected two 2.5-cm diameter cores (4.9 cm^2 area) adjacent to each of the larger cores. These smaller cores were used to determine sediment organic content and grain size. As with the larger cores, they were divided into two 2.5-cm thick sections. Each section was placed in a separate plastic bag, labelled, and stored on ice until it could be frozen (generally within 8 hours) for later analysis.

In the laboratory, I separated animals, shells, and debris from macroorganic matter collected in the 10-cm cores. I identified macroinfauna to species or the lowest feasible taxonomic level for enumeration and then dried all organisms (mollusks were removed from their shells) to a constant weight at 100°C. The macroorganic

matter (MOM) in these samples consisted of roots, rhizomes, and detritus retained on a 0.5-mm mesh sieve, and was divided into two categories, live (LMOM) and dead or detrital (DMOM). LMOM (*Spartina* roots and rhizomes which appeared to have been alive at the time of collection) was separated from DMOM (dead roots and rhizomes, as well as other detritus) under a dissecting microscope. Both LMOM and DMOM were then dried to a constant weight at 100°C. Weights for MOM are the combined weights of the LMOM and DMOM. Sediment organic content (SOC) was determined from one of the 2.5-cm diameter cores by measuring the weight lost upon ignition (Dean 1974). The samples were dried for 24 hours, dry sieved through a 2-mm mesh to remove roots and shell, placed into pre-weighed ceramic crucibles, burned in a muffle furnace at 400°C for 4 hours, and re-weighed.

In addition, I analyzed the SOC samples taken during winter 1993 and spring 1993 using the rapid oxidation technique described by Sims and Haby (1971). I added 10 ml of $K_2Cr_2O_7$ and 10 ml H_2SO_4 to 1 g of sediment, allowed 20 minutes reaction time, diluted to 100 ml with deionized water, centrifuged for 15 minutes, and measured the absorption of the supernatant at 600 nm using a Beckman DU6000 spectrophotometer. Absorption values were

compared to a standard curve, which had been prepared by following the above procedure on pre-ignited sediments containing calculated amounts of sucrose.

From the remaining 2.5-cm core, I determined the percentage of sand, silt, and clay in the sediments of the samples taken during winter 1993 and fall 1993, using the sieving and settling techniques described by Folk (1980).

Following initial analysis of vertical distribution of infauna and other sediment parameters, I combined data from the two vertical sections in each core. The remaining analyses were conducted as if a 5-cm deep core was collected. These combined data, therefore, are comparable to other data collected with a single 5-cm deep sediment core.

Infauna and macroorganic matter samples taken between *Spartina* stems during fall and spring from the 83Marsh and 87Marsh were compared to data collected in these same marshes and in a nearby natural marsh as part of a study conducted in 1990/1991.

Statistical Analysis

Statistical analyses were conducted using separate ANOVA models for each sampling period. I designed the

initial analysis to examine the vertical distribution of infauna in the sediment cores, and the completely-randomized factorial ANOVA model had four main effects: Marsh (83Marsh, 87Marsh, 92Marsh), Elevation (edge, inner), Proximity to stems (near stems, between stems), and Vertical distribution (upper 2.5 cm, lower 2.5 cm). Data from the upper and lower sections of the cores were then combined, and I used a three factorial ANOVA model to examine the main effects of Marsh, Elevation, and Proximity. A ln (Y+1) transformation was used on animal density data in all ANOVAs to correct a positive relationship between cell means and standard deviations; transformed density data are presented graphically throughout the paper. Within main effects and first-order interactions, I used *a priori* contrasts to compare means from the 92Marsh with means from both older marshes.

I calculated a correlation matrix to identify autocorrelated variables and then used stepwise regression analysis to identify factors related to the abundance of infaunal organisms in the marshes. I used a forward selection technique, with a partial F-ratio of 4.0 to enter the model and of 3.996 to remove a variable. Independent variables were ASH, LMOM, and DMOM, for the four seasons, and DIG and CLAY for the sampling periods

where data were available. Dependent variables included, biomass and abundance of total infauna, as well as the abundance of *Streblospio benedicti*, *Capitella capitata*, and crustaceans. Abundance data were transformed using an ln(y+1) transformation. I also examined the effects of elevation, proximity to stems, and marsh on sediment-infauna relationships.

Throughout these analyses, a probability value of < 0.05 was considered statistically significant. Analyses were conducted using the SuperANOVA and Statview software packages (Abacus Concepts, Inc., Berkeley, CA, 1989).

Data collected from experimental marshes were compared to data collected from five nearby natural marshes using ANOVA. The methods for that study are detailed in Minello and Webb (in review).

RESULTS

Characterization of the Infauna

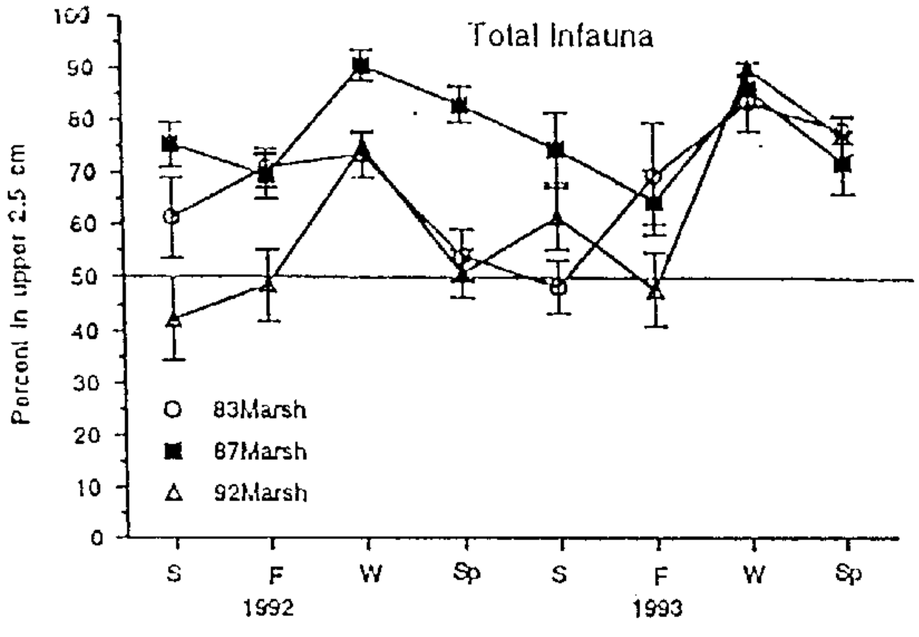
Macroinfauna collected in marsh sediments were dominated by annelid worms (92.5% of infauna), and most of these were polychaetes (Table 1). Abundant polychaetes included surface deposit feeders and suspension feeders such as *Streblospio benedicti* (42.8% of polychaetes), *Tharyx marioni* (13.5%), and *Polydora ligni* (9.1%); the subsurface deposit feeder *Capitella capitata* (18.4%); and the omnivore *Neanthes succinea* (10.0%). *S. benedicti* was the dominant species in both older marshes, but *C. capitata* was the most abundant organism found in the 92Marsh. Over the two years of sampling, I identified 46 species of polychaetes in the marshes; 36 of these species were found in the 83Marsh, 24 in the 87Marsh and 33 in the 92Marsh. Oligochaetes were not abundant, making up only 3.6% of the annelids. Crustaceans made up 6.6% of the infauna in sediments, and most crustaceans were amphipods (Table 1). In relation to their abundance, diversity in this group was high (34 crustacean species identified overall); and I identified 26 species in the 83Marsh, 24 in the 87Marsh, and 21 in the 92Marsh. Mollusks were rare in marsh sediments and composed mostly of small bivalves.

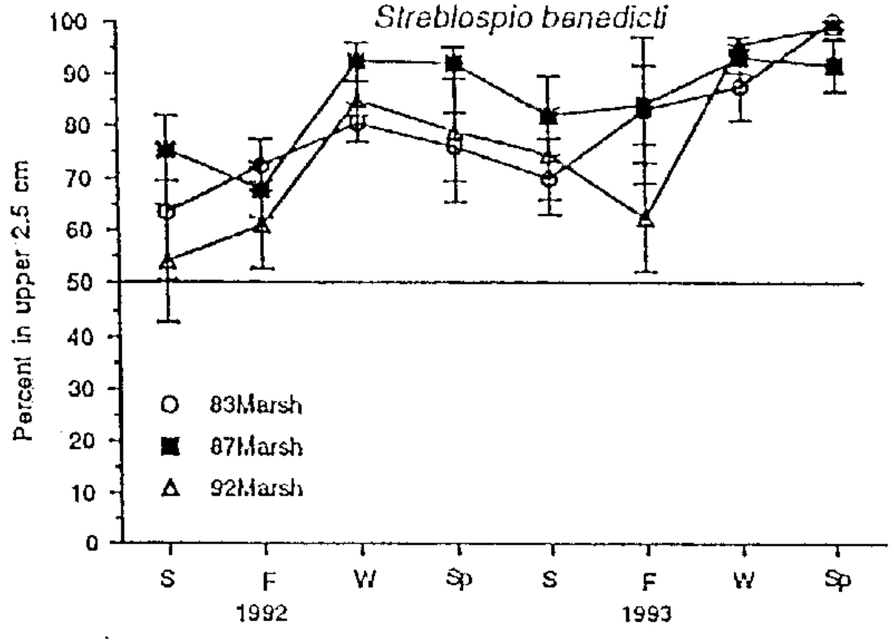
TABLE 1. Common macrofauna collected in sediment cores from the three created marshes located on Pelican Spit. Sampling was conducted quarterly for two years, beginning in July 1992. Mean densities (untransformed) with standard errors are shown for each marsh. Species are listed if over 20 individuals were collected and are ranked within major groups according to their overall abundance. The collection represents 384 cores (each 78.5 cm^2, 5 cm deep) (total n=384,total area sampled=3 m^2), and 128 cores (1 m^2 of area)were collected in each marsh. Species richness is indicated by the total number of species collected in each marsh. Polychaetes have also been assigned to feeding groups according to Gaston and Nasci (1988). These groups include carnivores (C), omnivores (O), surface-deposit feeders (SDF), subsurface deposit feeders (SsDF), and suspension feeders(SuF).

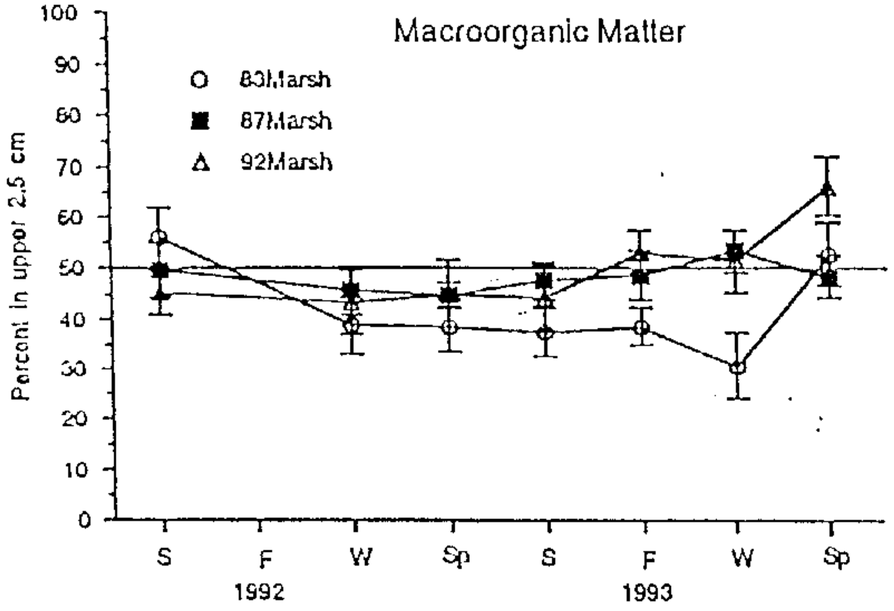
Species / taxon	Feeding group	83Marsh Mean	83Marsh SE	87Marsh Mean	87Marsh SE	92Marsh Mean	92Marsh SE	Total Number Collected
Total Infauna		85.9	9.59	53.7	5.51	72.1	6.25	27092
Annelids		81.9	9.24	48.7	4.93	65.2	5.13	25062
Polychaetes		79.5	9.21	44.8	4.70	64.3	5.06	24150
Streblospio benedicti	SDF/SuF	37.0	6.38	25.4	2.88	18.4	2.29	10346
Capitella capitata	SsDF	10.1	1.83	3.0	0.41	21.7	2.50	4448
Tharyx marioni	SDF	13.4	2.56	2.1	0.62	9.9	2.35	3264
Nereis (Neanthes) succinea	C	7.6	0.99	5.1	0.93	6.2	0.81	2416
Polydora ligni	SDF/SuF	7.1	2.00	6.2	1.57	3.8	1.01	2193
Mediomastus spp.	SsDF	1.0	0.29	0.5	0.18	1.4	0.24	375
Heteromastus filiformis	SsDF	1.7	0.23	0.5	0.11	0.5	0.12	349
Parandalia ocularis	O	0.2	0.07	0.7	0.29	0.3	0.09	161
Mediomastus californiensis	SsDF	0.3	0.08	0.3	0.10	0.5	0.14	148
Laeonereis culveri	C	0.0	0.01	0.0	0.02	0.5	0.22	77
Polydora cf. socialis	SDF/SuF	0.0	0.01	0.6	0.32	0.0	0.00	72
Eteone heteropoda	C	0.4	0.07	0.1	0.04	0.0	0.02	69
Leitoscoloplos fragilis	SsDF	0.2	0.07	0.0	0.02	0.3	0.08	67
Aricidea philbana	SsDF	0.1	0.03	0.0	0.00	0.1	0.04	21
No. Polychaete species		36		24		33		46
Oligochaetes		2.3	0.49	3.9	0.93	0.9	0.27	912
Crustaceans		3.4	0.67	4.5	1.31	6.1	2.07	1780
Gammarus mucronatus		2.4	0.57	1.6	0.69	4.9	1.79	1144
Corophium spp.		0.5	0.13	1.8	0.71	0.5	0.16	357
Uca spp.		0.0	0.02	0.5	0.17	0.1	0.04	82
No. Crustacean species		28		24		21		34
Molluscs		0.5	0.07	0.2	0.04	0.4	0.10	145
No. Mollusc species		11		7		7		15
Others (includes fish)		0.2	0.13	0.2	0.04	0.4	0.11	98

Vertical Distribution

Each 5-cm deep sediment core was divided into an upper and lower 2.5-cm section, and initially these sections were analyzed separately. Overall, most infauna (74%) were found in the upper half of the cores. There was some indication of seasonality in the distribution of infauna with highest percentages in upper sediments generally occurring in winter (Fig. 2). However, the mean number of infauna in the upper half of the core was higher than in the lower half for every sampling period, and differences were statistically significant for six of the eight sampling periods. The 92Marsh generally had more infauna in the lower half of the cores than the two older marshes, as evidenced by significant interactions between Vertical distribution and Marsh in the ANOVA for the first five sampling periods. In part, this pattern was due to the relatively high abundance of *C. capitata* in the 92Marsh; this species was more evenly distributed in the sediment than *S. benedicti*, the dominant species in the older marshes (Fig. 2). *S. benedicti* was mainly found (78%) in the upper half of the sediment cores. Crustaceans were also found mostly near the sediment water interface; 94% of crustaceans were in the upper half of the cores. Macroorganic matter was evenly







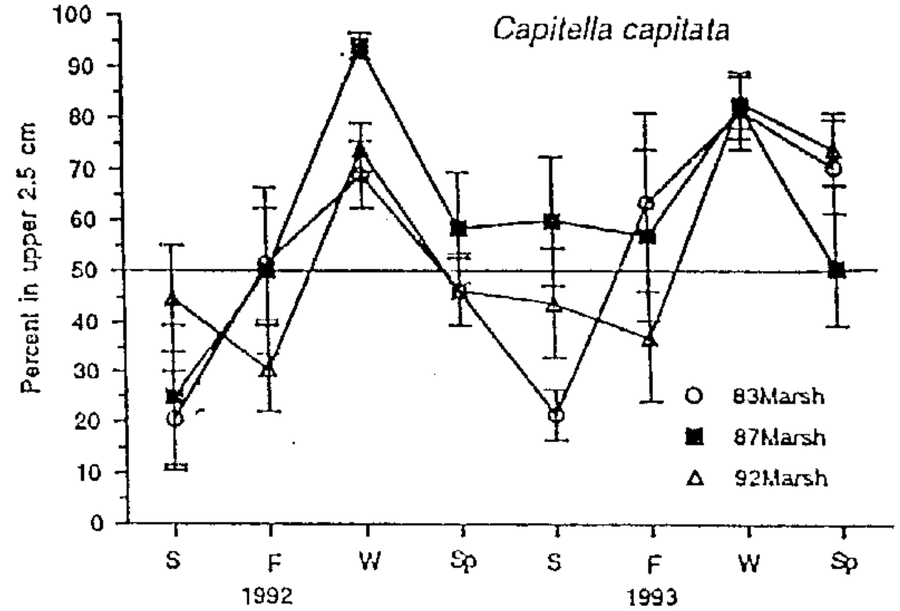


Fig. 2. Percentage of infauna (based on density) and macroorganic matter in upper 2.5 cm of sediment cores over the eight seasonal sampling periods in each marsh.

distributed between the upper and lower sections of the cores (Fig. 2). The vertical distribution of infauna did not appear to be strongly affected by marsh elevation, and for total infauna this interaction was only significant in the ANOVAs during one of the eight sampling period.

Most studies of macroinfauna abundance use integrated data from at least the upper 5 cm of sediment. Therefore, I combined the data from the upper and lower core sections and conducted all remaining analyses as if 5-cm deep cores were collected and analyzed. This consolidation of the data simplified analysis of marsh effects and facilitated density comparisons with other research studies.

Overall Comparisons Among Marshes

Infaunal abundance and biomass were generally highest in winter and spring in all three marshes (Fig. 3). Total infaunal abundance differed among the three marshes during all but the fall 1992 and summer 1993 sampling periods (main effect of Marsh, Table 2), but none of the marshes consistently supported the highest density of animals. Total infaunal abundance in the 92Marsh was often statistically different from densities in the other marshes (Table 2); but in seven of

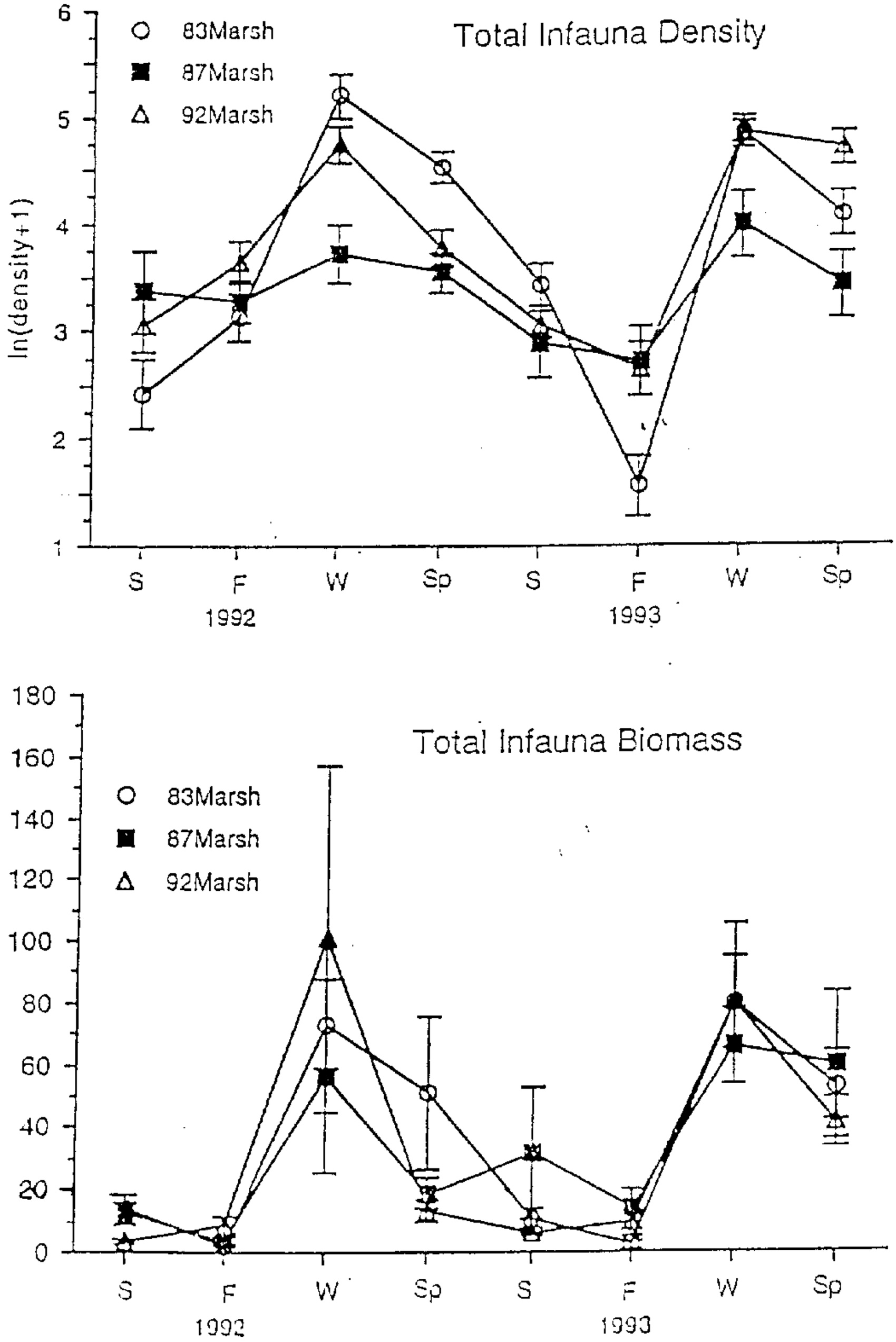


Fig. 3. Mean (+/- 1 SE) density (ln transformed) and biomass of total infauna at the three created marshes on Pelican Spit for the eight seasonal sampling periods. Values are from 78.5-cm² sediment cores.

TABLE 2. ANOVA results examining the effects of Marsh, Elevation, and Proximity to *Spartina alterniflora* stems. The degrees of freedom, sum of squares, and probability values are shown for main effects, 2-way interactions, and *a priori* contrasts. Contrasts within the Marsh effect and Marsh interactions compare means from the 92Marsh (92) with the 83(Marsh) (83) and the 87Marsh (87).

Density of Total Infauna

		Summer 1992		Fall 1992		Winter 1992/93		Spring 1993		Summer 1993		Fall 1993		Winter 1993/94		Spring 1994	
EFFECT	df	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P
MARSH	2	7.32	0.005	2.31	0.055	18.62	0.000	8.54	0.000	2.37	0.104	13.64	0.001	7.99	0.000	13.08	0.000
92 v 83	1	3.21	0.026	2.17	0.020	1.68	0.054	4.68	0.000	1.10	0.144	9.42	0.001	0.00	0.989	3.14	0.005
92 v 87	1	0.74	0.271	1.14	0.088	8.50	0.000	0.39	0.214	0.21	0.521	0.06	0.780	5.93	0.001	13.08	0.000
ELEVATION	1	33.08	0.000	1.87	0.030	3.52	0.007	0.23	0.336	2.33	0.038	22.39	0.000	5.06	0.001	0.00	0.989
PROXIMITY TO STEMS	1	7.19	0.001	5.05	0.001	3.55	0.006	2.01	0.007	7.93	0.000	2.31	0.090	2.11	0.030	11.50	0.000
Marsh v Elevation	2	5.08	0.021	4.27	0.006	8.63	0.000	8.64	0.000	2.57	0.086	1.07	0.500	8.92	0.000	3.59	0.011
Edge																	
92 v 83	1	0.48	0.375	0.01	0.874	3.32	0.008	4.60	0.000	0.57	0.287	5.62	0.010	0.04	0.751	5.64	0.000
92 v 87	1	4.77	0.007	0.37	0.322	0.00	0.987	1.82	0.010	0.45	0.345	0.47	0.438	0.04	0.765	8.17	0.000
Inner																	
92 v 83	1	3.39	0.022	4.74	0.001	0.00	0.988	0.83	0.075	0.52	0.309	3.88	0.030	0.03	0.792	0.02	0.828
92 v 87	1	0.94	0.217	4.50	0.001	17.09	0.000	5.00	0.000	1.72	0.069	0.11	0.701	13.23	0.000	8.92	0.000
Marsh v Proximity	2	3.16	0.082	2.84	0.030	1.23	0.248	0.02	0.965	9.18	0.001	2.91	0.162	0.70	0.442	4.53	0.004
Stems																	
92 v 83	1	0.01	0.895	2.19	0.019	0.36	0.362	2.29	0.004	2.80	0.022	1.10	0.237	0.12	0.591	0.08	0.643
92 v 87	1	0.59	0.323	3.75	0.003	8.06	0.000	0.14	0.462	3.30	0.014	1.25	0.207	3.90	0.004	1.16	0.078
No Stems																	
92 v 83	1	5.91	0.003	0.36	0.328	1.52	0.068	2.37	0.004	0.04	0.783	10.83	0.001	0.10	0.629	4.96	0.001
92 v 87	1	0.20	0.566	0.18	0.489	1.65	0.058	0.27	0.303	6.04	0.001	0.60	0.381	2.16	0.028	16.30	0.000
Elevation v Proximity	1	0.06	0.749	0.03	0.771	1.56	0.063	0.11	0.503	0.11	0.639	1.33	0.194	0.03	0.780	1.21	0.072
Residual error	2	21.32		13.19		15.20		8.85		17.65		27.34		14.76		12.65	

TABLE 2. Continued

Biomass of Total Infauna (mg dry wt)

EFFECT	df	Summer 1992 SS	Summer 1992 P	Fall 1992 SS	Fall 1992 P	Winter 1992/93 SS	Winter 1992/93 P	Spring 1993 SS	Spring 1993 P	Summer 1993 SS	Summer 1993 P	Fall 1993 SS	Fall 1993 P	Winter 1993/94 SS	Winter 1993/94 P	Spring 1994 SS	Spring 1994 P
MARSH	2	983.20	0.014	405.13	0.021	16019.66	0.693	13028.22	0.155	6006.08	0.316	1054.63	0.202	1972.95	0.715	2778.01	0.381
92 v 83	1	602.00	0.008	379.50	0.007	6105.13	0.598	11188.34	0.074	121.68	0.828	408.27	0.283	0.05	0.997	1075.32	0.387
92 v 87	1	632.79	0.017	199.50	0.047	15899.92	0.399	246.98	0.786	5176.53	0.161	141.98	0.507	1471.53	0.481	2717.69	0.172
ELEVATION	1	585.20	0.021	0.81	0.910	1887.44	0.781	154.80	0.830	3933.13	0.220	18.63	0.809	20053.28	0.013	8891.69	0.016
PROXIMITY TO STEMS	1	1570.84	0.000	49.21	0.313	18208.75	0.392	9941.76	0.092	3843.13	0.225	1592.76	0.031	58457.50	0.000	44658.10	0.000
Marsh v Elevation	2	312.29	0.225	16.43	0.840	63282.43	0.244	9865.45	0.239	3796.35	0.479	508.49	0.458	24627.18	0.022	28487.83	0.001
Edge																	
92 v 83	1	1056.25	0.003	132.83	0.101	2719.82	0.725	730.35	0.642	26.78	0.920	184.98	0.449	6834.10	0.140	922.64	0.422
92 v 87	1	807.62	0.019	108.16	0.138	7726.41	0.553	1012.83	0.584	141.81	0.814	25.00	0.780	17702.30	0.019	9853.06	0.013
Inner																	
92 v 83	1	57.00	0.458	256.80	0.025	28455.02	0.278	15018.50	0.040	108.88	0.837	224.25	0.405	8883.06	0.138	5890.56	0.048
92 v 87	1	119.38	0.283	91.68	0.171	70278.01	0.080	92.16	0.869	8073.02	0.082	477.42	0.227	8209.44	0.153	601.48	0.516
Marsh v Proximity	2	1111.02	0.008	134.91	0.251	66940.40	0.226	7091.81	0.354	3840.01	0.475	644.37	0.370	9279.29	0.217	9438.89	0.046
Stems																	
92 v 83	1	1898.80	0.000	323.10	0.013	10593.58	0.488	17483.45	0.028	531.30	0.649	567.63	0.188	118.81	0.841	3378.52	0.129
92 v 87	1	848.64	0.004	331.24	0.012	4914.01	0.638	887.75	0.851	8850.11	0.069	283.08	0.350	6400.00	0.147	11140.80	0.008
No Stems																	
92 v 83	1	12.25	0.729	91.68	0.171	45550.23	0.155	301.02	0.785	55.50	0.883	22.56	0.791	112.36	0.845	138.06	0.755
92 v 87	1	22.80	0.637	3.15	0.707	61157.29	0.101	16.00	0.945	58.91	0.880	0.00	0.999	663.06	0.636	1012.83	0.401
Elevation v Proximity	1	828.34	0.007	1.76	0.847	97812.98	0.040	1144.65	0.560	1135.88	0.507	205.43	0.425	11491.74	0.054	11319.09	0.007
Residual error	2	3613.62		1688.90		776889.08		119305.40		90953.37		11352.00	0.295	104670.28		50395.81	

TABLE 2. Continued

Density of Streblospio benedicti

		Summer 1992		Fall 1992		Winter 1992/93		Spring 1993		Summer 1993		Fall 1993		Winter 1993/94		Spring 1994	
EFFECT	df	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P
MARSH	2	19.69	0.000	2.06	0.173	14.23	0.003	47.06	0.000	2.23	0.346	16.44	0.001	9.85	0.019	7.43	0.023
92 v 83	1	3.57	0.023	0.81	0.301	12.09	0.001	42.83	0.000	1.95	0.176	11.45	0.001	1.27	0.280	5.00	0.023
92 v 87	1	6.41	0.003	0.42	0.391	0.22	0.641	25.53	0.000	0.06	0.817	0.06	0.797	3.89	0.069	0.05	0.806
ELEVATION	1	84.20	0.000	3.05	0.025	0.42	0.526	0.29	0.521	11.65	0.002	28.92	0.000	5.86	0.027	13.46	0.000
PROXIMITY TO STEMS	1	0.58	0.355	2.36	0.047	4.07	0.052	0.08	0.733	1.94	0.176	0.82	0.339	1.14	0.317	2.28	0.118
Marsh v Elevation	2	0.18	0.868	7.71	0.003	8.99	0.019	0.46	0.717	5.89	0.069	4.41	0.095	9.91	0.018	5.76	0.051
Edge																	
92 v 83	1	2.18	0.072	1.87	0.092	14.91	0.001	17.76	0.000	5.33	0.028	7.48	0.008	1.52	0.248	1.75	0.170
92 v 87	1	3.82	0.018	3.85	0.013	5.82	0.022	12.80	0.000	3.15	0.087	1.57	0.190	0.51	0.501	3.05	0.072
Inner																	
92 v 83	1	1.43	0.142	5.76	0.003	1.11	0.301	25.42	0.000	0.11	0.742	4.20	0.035	0.13	0.733	3.38	0.059
92 v 87	1	2.65	0.049	1.09	0.171	3.04	0.091	12.73	0.000	2.08	0.161	0.83	0.338	12.27	0.002	2.01	0.142
Marsh v Proximity	2	2.01	0.219	4.34	0.030	5.09	0.094	0.59	0.656	3.64	0.182	0.40	0.799	2.74	0.301	0.93	0.598
Stems																	
92 v 83	1	0.35	0.462	2.78	0.032	7.42	0.010	25.48	0.000	1.48	0.237	4.31	0.033	2.58	0.135	2.47	0.104
92 v 87	1	2.49	0.055	0.87	0.219	0.80	0.378	16.64	0.000	2.05	0.165	0.00	0.951	2.98	0.110	0.58	0.428
No Stems																	
92 v 83	1	4.33	0.013	0.31	0.460	4.81	0.036	17.71	0.000	0.57	0.458	7.34	0.008	0.00	0.990	2.52	0.101
92 v 87	1	4.01	0.017	3.43	0.018	2.45	0.128	9.40	0.001	1.21	0.283	0.08	0.763	1.14	0.316	0.18	0.652
Elevation v Proximity	1	1.20	0.177	0.06	0.755	0.40	0.535	0.20	0.598	2.61	0.118	0.41	0.497	1.41	0.266	0.01	0.922
Residual error	2	22.88		20.09		38.36		24.77		36.89		31.54		39.75		32.03	

TABLE 2. Continued

Density of Capitella capitata

EFFECT	df	Summer 1992		Fall 1992		Winter 1992/93		Spring 1993		Summer 1993		Fall 1993		Winter 1993/94		Spring 1994	
		SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P
MARSH	2	14.84	0.000	27.87	0.000	53.90	0.000	24.99	0.000	0.35	0.789	1.85	0.108	19.24	0.000	17.33	0.000
92 v 83	1	8.78	0.001	12.74	0.000	4.60	0.016	1.08	0.189	0.23	0.580	1.30	0.076	12.49	0.000	10.29	0.000
92 v 87	1	14.14	0.000	26.58	0.000	51.16	0.000	22.81	0.000	0.30	0.532	1.48	0.060	18.14	0.000	15.22	0.000
ELEVATION	1	1.06	0.158	3.25	0.006	0.32	0.508	7.95	0.001	7.87	0.003	0.14	0.554	6.97	0.001	35.99	0.000
PROXIMITY TO STEMS	1	1.36	0.112	4.19	0.002	0.27	0.542	3.81	0.012	2.18	0.095	0.14	0.554	0.01	0.888	3.50	0.015
Marsh v Elevation	2	7.04	0.003	4.81	0.004	13.18	0.001	11.88	0.000	3.42	0.115	1.01	0.285	12.28	0.000	19.19	0.000
Edge																	
92 v 83	1	0.39	0.388	7.81	0.000	2.60	0.065	1.13	0.159	0.09	0.726	0.20	0.478	4.54	0.008	0.52	0.331
92 v 87	1	0.88	0.262	6.04	0.000	8.32	0.002	2.08	0.080	1.10	0.232	0.02	0.819	0.29	0.487	0.12	0.647
Inner																	
92 v 83	1	9.38	0.000	5.07	0.001	2.02	0.102	0.18	0.588	0.97	0.261	1.38	0.070	8.22	0.001	14.55	0.000
92 v 87	1	20.29	0.000	23.34	0.000	52.30	0.000	27.97	0.000	0.08	0.749	2.48	0.017	26.49	0.000	34.30	0.000
Marsh v Proximity Stems	2	0.81	0.557	1.77	0.110	2.59	0.178	0.79	0.493	5.24	0.040	0.18	0.798	1.49	0.288	0.14	0.880
92 v 83	1	3.73	0.010	9.98	0.000	8.04	0.006	0.28	0.478	1.55	0.157	1.14	0.095	5.45	0.004	8.19	0.002
92 v 87	1	10.08	0.000	20.83	0.000	37.00	0.000	14.28	0.000	4.00	0.026	0.75	0.174	12.20	0.000	7.53	0.001
No Stems																	
92 v 83	1	3.07	0.019	3.58	0.004	0.33	0.501	0.88	0.213	0.32	0.516	0.30	0.389	7.09	0.001	4.20	0.008
92 v 87	1	4.59	0.005	7.42	0.000	16.26	0.000	8.69	0.000	1.51	0.162	0.71	0.184	4.79	0.007	7.89	0.001
Elevation v Proximity	1	0.03	0.801	0.01	0.877	2.87	0.053	0.05	0.777	0.20	0.605	0.17	0.513	0.04	0.805	0.01	0.884
Residual error	2	18.39		13.58		25.75		19.74		26.72		14.02		20.81		19.38	

TABLE 2. Continued

Density of Crustaceans

EFFECT	df	Summer 1992 SS	Summer 1992 P	Fall 1992 SS	Fall 1992 P	Winter 1992/93 SS	Winter 1992/93 P	Spring 1993 SS	Spring 1993 P	Summer 1993 SS	Summer 1993 P	Fall 1993 SS	Fall 1993 P	Winter 1993/94 SS	Winter 1993/94 P	Spring 1994 SS	Spring 1994 P
MARSH	2	4.22	0.000	0.92	0.280	2.78	0.132	2.53	0.109	1.35	0.114	4.09	0.008	13.20	0.000	1.53	0.331
92 v 83	1	1.00	0.005	0.87	0.122	0.24	0.551	1.17	0.149	0.63	0.149	0.00	0.960	9.26	0.001	0.81	0.279
92 v 87	1	4.22	0.000	0.42	0.278	1.30	0.188	0.22	0.528	1.28	0.044	3.12	0.005	0.04	0.811	1.41	0.158
ELEVATION	1	0.74	0.015	1.01	0.098	4.48	0.013	8.39	0.002	0.80	0.108	0.06	0.693	5.28	0.009	3.22	0.035
PROXIMITY TO STEMS	1	0.02	0.676	2.88	0.007	42.40	0.000	14.09	0.000	0.80	0.108	5.93	0.000	19.58	0.000	19.18	0.000
Marsh v Elevation	2	0.58	0.090	2.91	0.024	0.95	0.488	1.27	0.320	0.12	0.809	0.41	0.555	0.68	0.610	4.06	0.081
Edge																	
92 v 83	1	1.54	0.001	0.20	0.453	1.08	0.210	1.62	0.091	0.20	0.412	0.00	0.943	4.64	0.013	3.76	0.023
92 v 87	1	2.76	0.000	0.25	0.399	0.27	0.523	0.37	0.412	0.30	0.315	0.75	0.149	0.42	0.439	0.98	0.234
Inner																	
92 v 83	1	0.03	0.809	3.13	0.005	0.12	0.672	0.07	0.728	0.48	0.218	0.00	1.000	4.62	0.013	0.45	0.421
92 v 87	1	1.54	0.001	2.03	0.021	1.19	0.184	0.00	0.940	1.10	0.080	2.66	0.009	0.13	0.682	0.47	0.409
Marsh v Proximity	2	0.02	0.835	1.40	0.150	5.80	0.021	2.51	0.112	0.71	0.307	1.48	0.132	2.33	0.195	0.70	0.599
Stems																	
92 v 83	1	0.63	0.024	2.24	0.018	0.18	0.603	0.32	0.448	0.72	0.124	0.09	0.808	8.75	0.001	1.50	0.143
92 v 87	1	2.21	0.000	0.85	0.128	8.13	0.004	1.92	0.067	1.94	0.014	3.15	0.005	0.13	0.668	1.27	0.177
No Stems																	
92 v 83	1	0.39	0.073	0.03	0.771	1.23	0.177	0.94	0.195	0.08	0.814	0.12	0.559	1.81	0.112	0.00	0.956
92 v 87	1	2.00	0.000	0.00	1.000	0.75	0.289	0.52	0.331	0.04	0.709	0.52	0.227	0.01	0.928	0.30	0.507
Elevation v Proximity	1	0.12	0.318	0.08	0.831	0.41	0.434	1.59	0.095	0.61	0.158	0.13	0.537	4.18	0.018	12.38	0.000
Residual error	2	4.06		12.55		23.33		19.38		10.48		12.42		24.50		24.13	

TABLE 2. Continued

Sediment Organic Content

EFFECT	df	Summer 1992		Fall 1992		Winter 1992/93		Spring 1993		Summer 1993		Fall 1993		Winter 1993/94		Spring 1994	
		SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P
MARSH	2	6.78	0.025	4.666	0.281	13.18	0.000	18.17	0.000	20.64	0.000	22.70	0.000	11.80	0.003	17.66	0.000
92 v 83	1	0.26	0.582	0.668	0.532	0.15	0.598	1.19	0.148	0.08	0.634	0.73	0.378	0.24	0.594	0.80	0.212
92 v 87	1	3.84	0.038	1.750	0.313	8.61	0.000	16.93	0.000	14.33	0.000	13.20	0.001	7.41	0.005	9.80	0.000
ELEVATION	1	8.92	0.002	0.012	0.932	0.82	0.000	9.10	0.000	15.92	0.000	20.88	0.000	10.14	0.001	6.67	0.001
PROXIMITY TO STEMS	1	0.51	0.438	0.069	0.840	1.21	0.138	0.48	0.354	0.43	0.273	0.48	0.471	0.00	0.997	1.04	0.156
Marsh v Elevation	2	17.21	0.000	1.130	0.716	14.89	0.000	17.67	0.000	24.39	0.000	30.13	0.000	21.73	0.000	12.27	0.000
Edge																	
92 v 83	1	1.09	0.259	1.602	0.335	0.04	0.793	0.78	0.242	0.39	0.299	0.00	0.957	2.81	0.087	0.34	0.418
92 v 87	1	2.04	0.128	0.730	0.513	0.05	0.751	0.15	0.601	0.29	0.370	0.23	0.615	0.38	0.508	0.01	0.893
Inner																	
92 v 83	1	0.11	0.721	0.012	0.933	0.12	0.629	0.44	0.377	0.05	0.710	1.33	0.233	5.73	0.013	0.47	0.337
92 v 87	1	17.82	0.000	1.033	0.437	19.19	0.000	29.45	0.000	34.89	0.000	31.60	0.000	10.45	0.001	18.77	0.000
Marsh v Proximity	2	3.46	0.139	0.186	0.846	2.04	0.157	1.42	0.285	2.16	0.058	2.38	0.280	2.47	0.245	0.51	0.802
Stems																	
92 v 83	1	0.43	0.474	0.218	0.720	0.09	0.677	0.14	0.611	0.00	0.966	0.13	0.707	0.52	0.436	0.23	0.496
92 v 87	1	5.49	0.014	0.558	0.568	1.40	0.110	11.29	0.000	3.65	0.003	12.22	0.001	4.61	0.025	3.50	0.012
No Stems																	
92 v 83	1	0.00	0.950	0.475	0.598	0.06	0.742	1.36	0.125	0.18	0.475	2.45	0.108	1.90	0.142	0.61	0.275
92 v 87	1	0.18	0.642	1.267	0.390	8.79	0.000	8.04	0.002	11.85	0.000	2.70	0.092	2.90	0.072	8.54	0.001
Elevation v Proximity	1	1.40	0.201	7.299	0.044	1.19	0.139	3.15	0.022	0.42	0.279	0.34	0.543	1.58	0.179	0.06	0.728
Residual error	2	29.83		60.251		18.80		19.74		12.57		32.47		29.43		17.79	

TABLE 2. Continued

Macroorganic Matter

		Summer 1992		Fall 1992		Winter 1992/93		Spring 1993		Summer 1993		Fall 1993		Winter 1993/94		Spring 1994	
EFFECT	df	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P
MARSH	2	86.41	0.000	13.28	0.012	17.49	0.034	23.98	0.001	5.88	0.121	17.29	0.009	21.21	0.000	13.97	0.000
92 v 83	1	82.76	0.000	10.16	0.009	13.54	0.022	7.35	0.029	3.64	0.105	7.01	0.043	0.12	0.648	0.24	0.522
92 v 87	1	38.48	0.004	9.75	0.010	12.88	0.026	23.88	0.000	5.07	0.057	16.81	0.003	17.20	0.000	11.93	0.000
ELEVATION	1	0.95	0.629	0.04	0.857	1.34	0.458	0.00	0.974	0.59	0.507	0.48	0.594	2.97	0.025	3.26	0.022
PROXIMITY TO STEMS	1	90.98	0.000	10.51	0.001	28.18	0.001	27.45	0.000	24.87	0.000	24.43	0.000	17.55	0.000	9.57	0.000
Marsh v Elevation	2	3.58	0.842	8.49	0.051	24.15	0.011	1.10	0.882	1.93	0.487	0.52	0.849	2.30	0.134	7.54	0.004
Edge																	
92 v 83	1	49.02	0.001	6.12	0.037	0.10	0.837	2.29	0.214	3.07	0.135	1.97	0.273	0.00	0.992	1.31	0.139
92 v 87	1	32.72	0.007	16.74	0.001	13.29	0.023	14.39	0.003	6.60	0.031	8.05	0.030	13.78	0.000	7.70	0.001
Inner																	
92 v 83	1	34.39	0.006	4.14	0.084	23.87	0.003	5.39	0.060	0.90	0.415	5.48	0.071	0.24	0.512	3.37	0.020
92 v 87	1	9.32	0.135	0.11	0.778	1.04	0.371	9.72	0.013	0.38	0.595	8.77	0.024	4.64	0.008	4.45	0.008
Marsh v Proximity	2	65.22	0.001	2.14	0.449	1.23	0.771	3.86	0.272	5.44	0.141	2.59	0.450	3.53	0.050	0.03	0.975
Stems																	
92 v 83	1	143.00	0.000	9.38	0.011	11.30	0.035	8.24	0.044	7.02	0.027	7.27	0.039	0.01	0.899	0.22	0.542
92 v 87	1	34.82	0.006	4.20	0.082	7.42	0.084	23.42	0.000	1.86	0.242	15.91	0.003	15.05	0.000	8.23	0.002
No Stems																	
92 v 83	1	0.82	0.653	2.10	0.214	3.40	0.238	1.79	0.271	0.00	0.966	1.10	0.411	0.33	0.441	0.05	0.787
92 v 87	1	8.25	0.159	5.80	0.048	5.34	0.141	4.30	0.091	3.31	0.121	3.27	0.159	3.94	0.011	5.71	0.003
Elevation v Proximity	1	0.90	0.984	0.14	0.744	4.04	0.198	1.95	0.251	0.00	0.965	1.73	0.303	1.25	0.137	3.11	0.028
Residual error	2	143.71		47.12		84.74		51.41		47.29		57.06		19.44		20.61	

TABLE 2. Continued

Percent Live Macroorganic Matter

EFFECT	df	Summer 1992		Fall 1992		Winter 1992/93		Spring 1993		Summer 1993		Fall 1993		Winter 1993/94		Spring 1994	
		SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P
MARSH	2	20008.67	0.000	10974.13	0.001	7383.42	0.000	10879.87	0.000	1848.16	0.282	4707.87	0.008	2243.37	0.132	5328.43	0.003
92 v 83	1	11110.93	0.000	10627.00	0.000	6837.77	0.000	10445.18	0.000	1504.12	0.120	2315.06	0.026	784.38	0.229	5195.63	0.001
92 v 87	1	18081.88	0.000	4580.44	0.011	3701.46	0.001	4143.23	0.005	887.15	0.229	334.11	0.383	363.89	0.410	2117.87	0.023
ELEVATION	1	570.70	0.219	231.62	0.549	1952.92	0.017	1070.20	0.131	688.84	0.288	482.98	0.295	180.98	0.580	307.34	0.373
PROXIMITY TO STEMS	1	12517.22	0.000	13614.13	0.000	15801.03	0.000	16302.44	0.000	18546.07	0.000	3181.11	0.010	8508.30	0.001	7084.91	0.000
Marsh v Elevation	2	2827.74	0.038	2505.55	0.153	10138.00	0.000	2238.52	0.008	4252.34	0.038	1977.30	0.114	5390.13	0.011	2444.30	0.051
Edge																	
92 v 83	1	8388.44	0.000	7084.82	0.002	30.53	0.757	5011.58	0.002	1248.58	0.155	3038.01	0.012	713.02	0.251	1051.87	0.104
92 v 87	1	17228.53	0.000	6810.38	0.002	3398.58	0.002	5435.01	0.001	4141.89	0.012	317.55	0.395	280.98	0.469	2395.37	0.016
Inner																	
92 v 83	1	3305.39	0.005	3811.21	0.019	12413.88	0.000	5437.98	0.001	380.74	0.428	187.57	0.535	4397.02	0.006	4830.95	0.001
92 v 87	1	3458.03	0.004	173.91	0.603	829.44	0.113	299.55	0.421	494.40	0.367	1907.07	0.042	104.35	0.658	260.50	0.412
Marsh v Proximity	2	2080.52	0.071	5074.34	0.027	6047.55	0.001	3490.38	0.030	1054.68	0.420	523.52	0.548	2823.03	0.098	1899.48	0.095
Stems																	
92 v 83	1	9627.04	0.000	1836.98	0.097	1489.38	0.037	1272.71	0.102	224.40	0.542	1491.50	0.070	231.57	0.510	3441.00	0.005
92 v 87	1	7703.13	0.000	4.75	0.931	117.56	0.545	95.38	0.649	3.52	0.939	7.88	0.893	1519.83	0.097	111.14	0.591
No Stems																	
92 v 83	1	2598.18	0.011	10594.07	0.000	6179.53	0.000	11850.50	0.000	1589.42	0.110	865.83	0.163	3005.78	0.022	1872.94	0.032
92 v 87	1	10464.27	0.000	9582.94	0.000	9588.82	0.000	6804.00	0.001	1935.78	0.079	821.25	0.174	144.18	0.603	2974.61	0.008
Elevation v Proximity	1	1233.73	0.074	831.87	0.259	6002.54	0.000	1670.41	0.062	495.05	0.367	7.60	0.895	3845.99	0.010	3058.98	0.007
Residual error	2	13151.99		22773.73		11320.37		18265.53		21348.88		15393.53		18855.20		13588.81	

eight such contrasts, densities in the 92Marsh were higher than in the older marsh. Infaunal biomass was significantly different among the marshes only during the first two sampling periods (Table 2). In summer 1992, the 92Marsh had a lower biomass than the other two marshes; but by fall 1992 the biomass in the 92Marsh was significantly higher than in the other marshes (Table 2; Fig. 3).

The abundance of *Streblospio benedicti* differed among the three marshes during every sampling period except fall 1992 and summer 1993 (Table 2). Densities in the 92Marsh were significantly higher than in the 83Marsh during three sampling periods and significantly lower during two sampling periods (Table 2; Fig. 4). For most sampling periods (six of eight), there was no significant difference between abundances in the 92Marsh and the 87Marsh, but abundances were significantly lower in the 92Marsh during two sampling periods. Densities of the other dominant polychaete, *Capitella capitata*, were generally highest in the 92Marsh and lowest in the 87Marsh (Table 1). Abundances in the 92Marsh were significantly higher than in the other two marshes for all 11 significant contrasts (Table 2; Fig. 4).

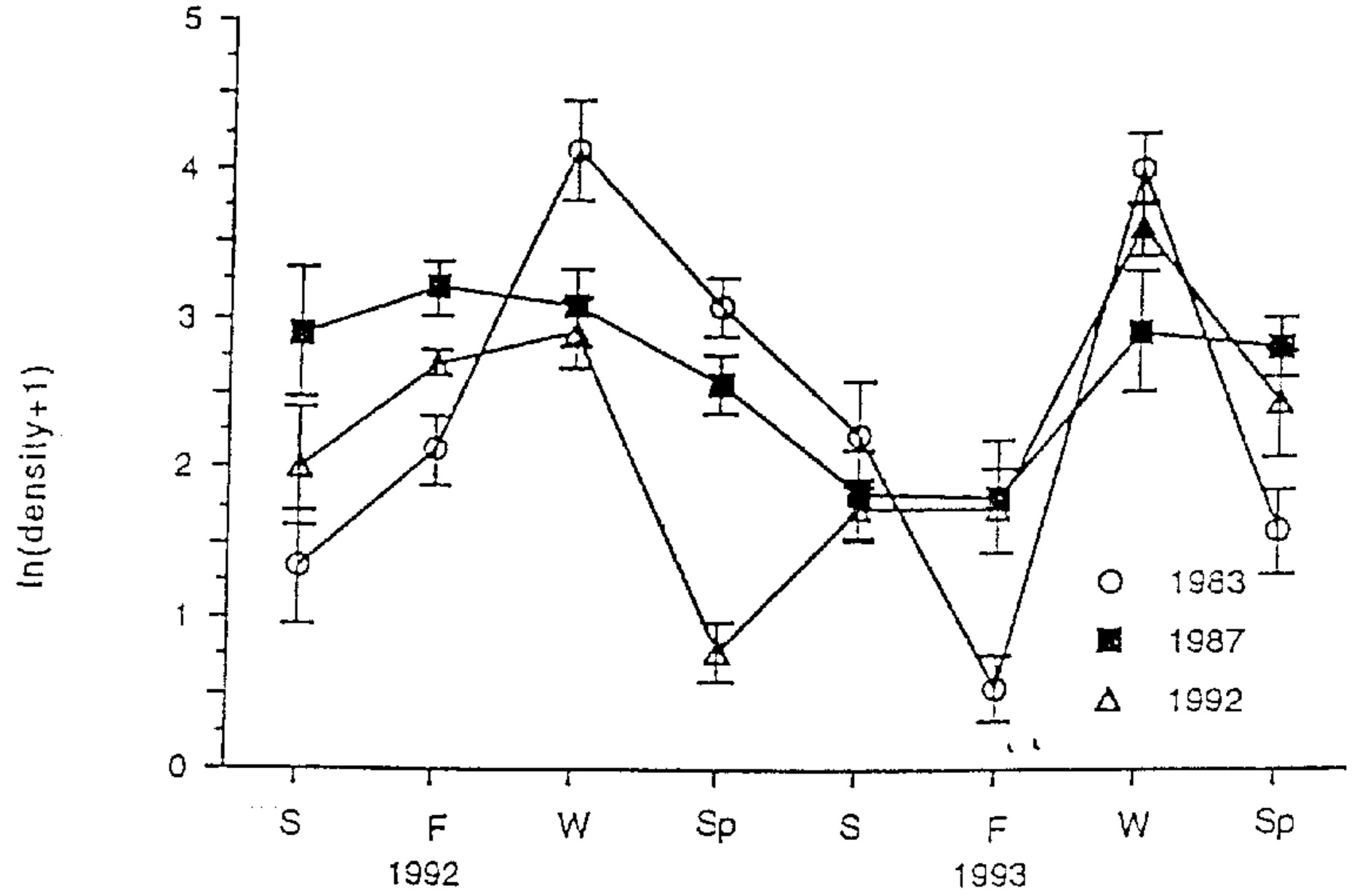
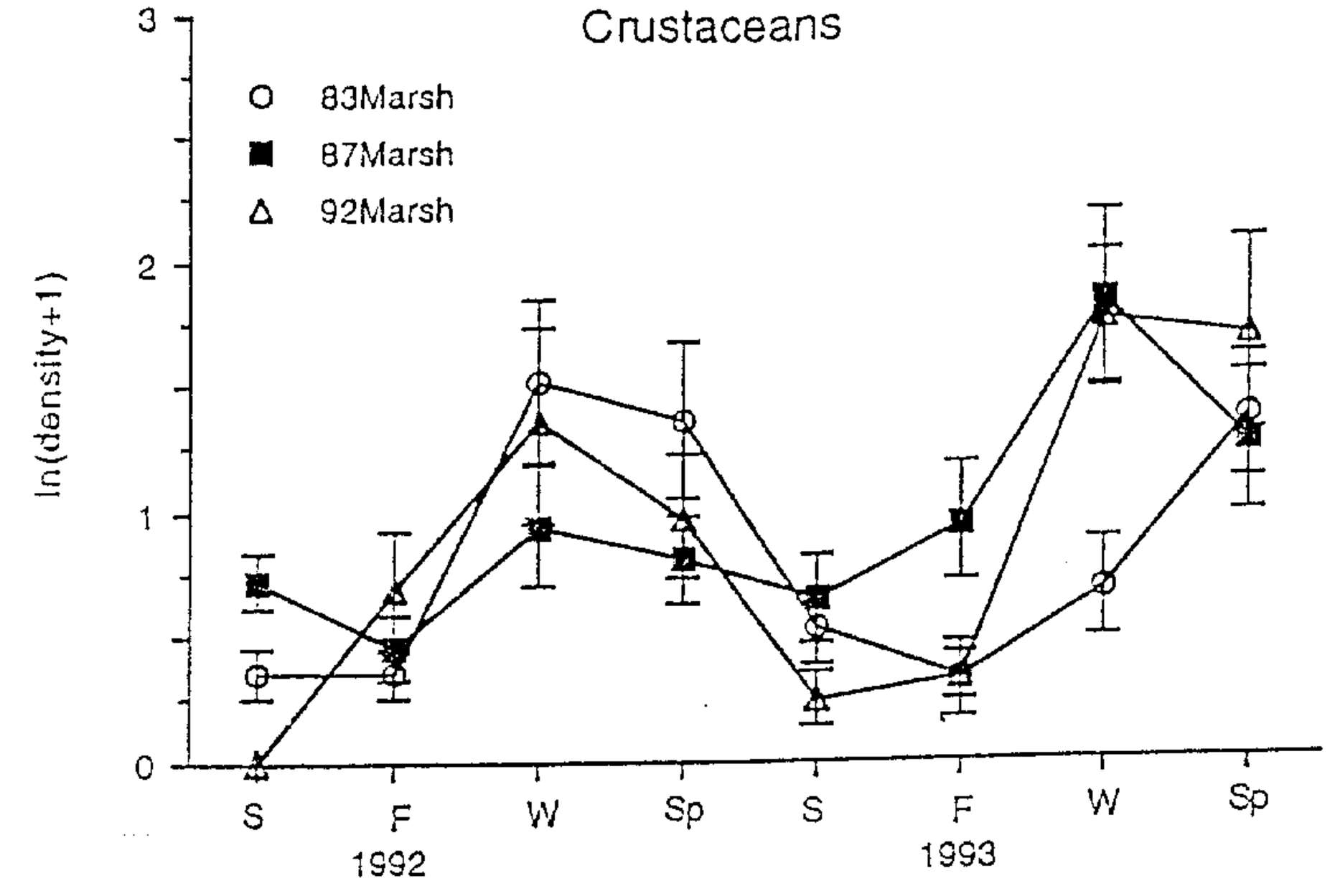


Fig. 4. Mean density (ln transformed) of the two most abundant species in the three marshes for the eight seasonal sampling periods.

The density of crustaceans was relatively low (Table 1), and variability in this group was high. Seasonal abundance peaks occurred in winter and spring (Fig. 5). During the first sampling period in summer 1992, crustacean densities were significantly lower in the 92Marsh than at both other marshes (Table 2; Fig. 5). In subsequent sampling, there was either no significant difference among the marshes or no consistent differences in densities of this group.

The 92Marsh differed from the two older marshes in the abundance of dominant species and in the overall trophic structure within the polychaetes. The 92Marsh was dominated by the subsurface deposit feeder, *Capitella capitata*, while the two other marshes were dominated by the surface deposit feeder, *Streblospio benedicti*. Overall, the percentage of subsurface deposit feeders was highest in the 92Marsh (Fig. 6).

Mean sediment organic content (SOC) in the three marshes was low and never exceeded 3% over the 2 years of sampling (Fig. 5). SOC in the 92Marsh was never significantly different from SOC in the 83Marsh but was significantly lower than in the 87Marsh for seven of eight sampling periods (Table 2). The mean weight of macroorganic matter (roots, rhizomes, and detritus



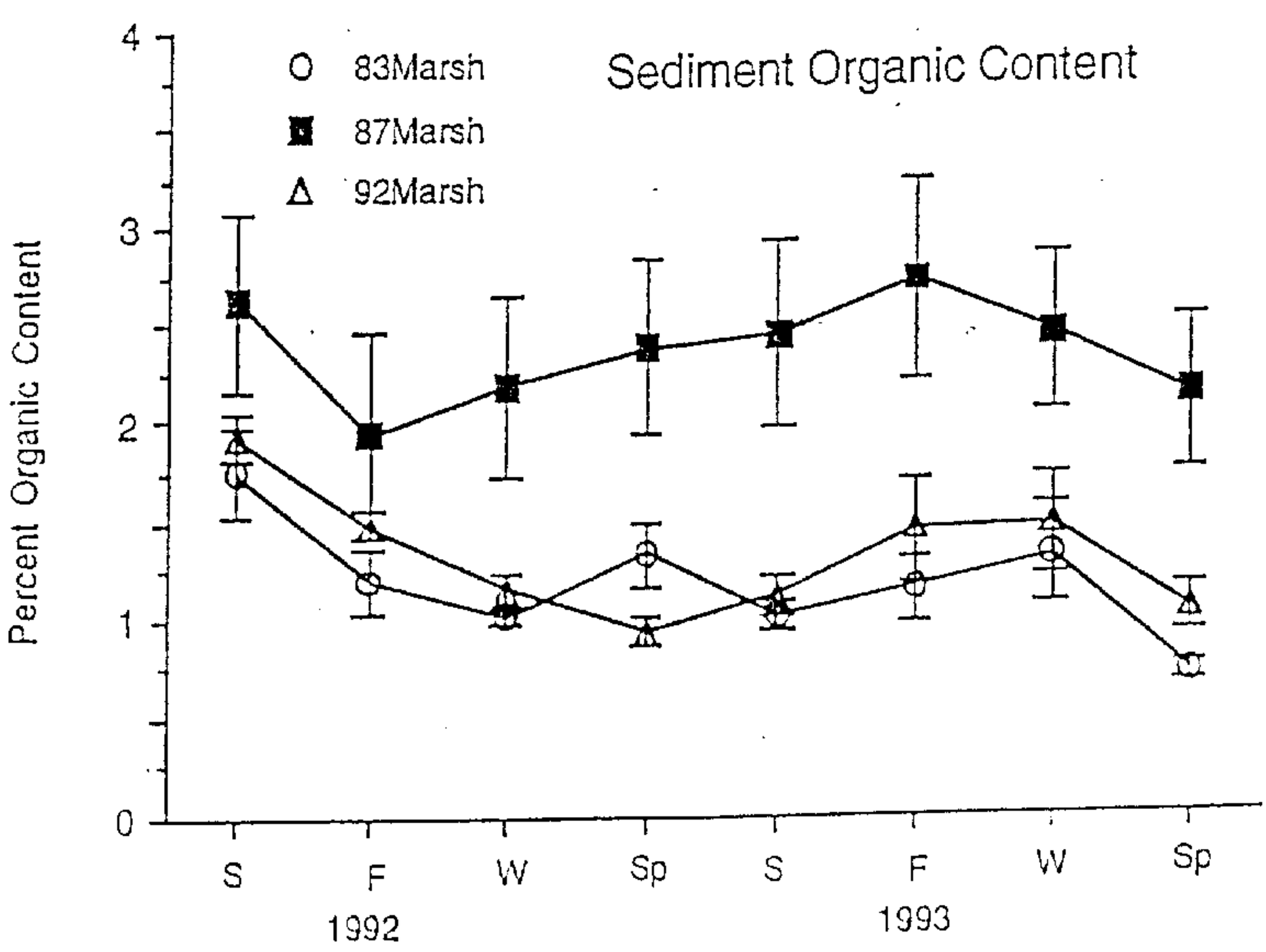


Fig. 5. Mean (+/- 1 SE) density (ln transformed) of total crustaceans (from 78.5-cm² sediment cores) and sediment organic content (% dry weight lost on ignition) at the three created marshes on Pelican Spit for the eight seasonal sampling periods.

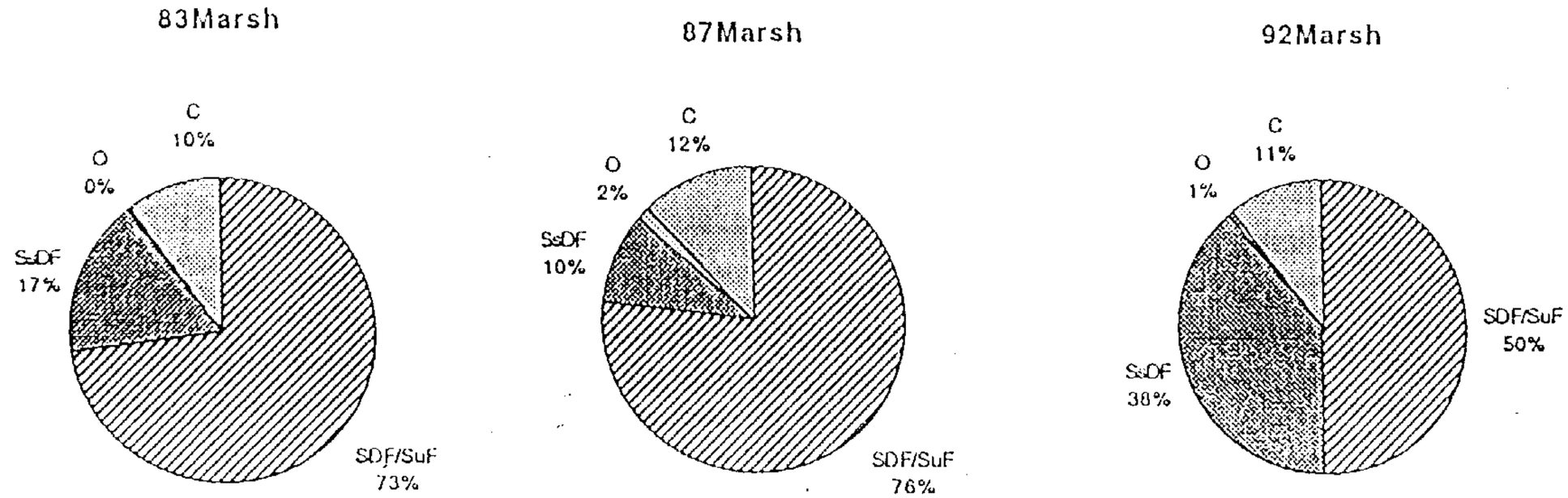
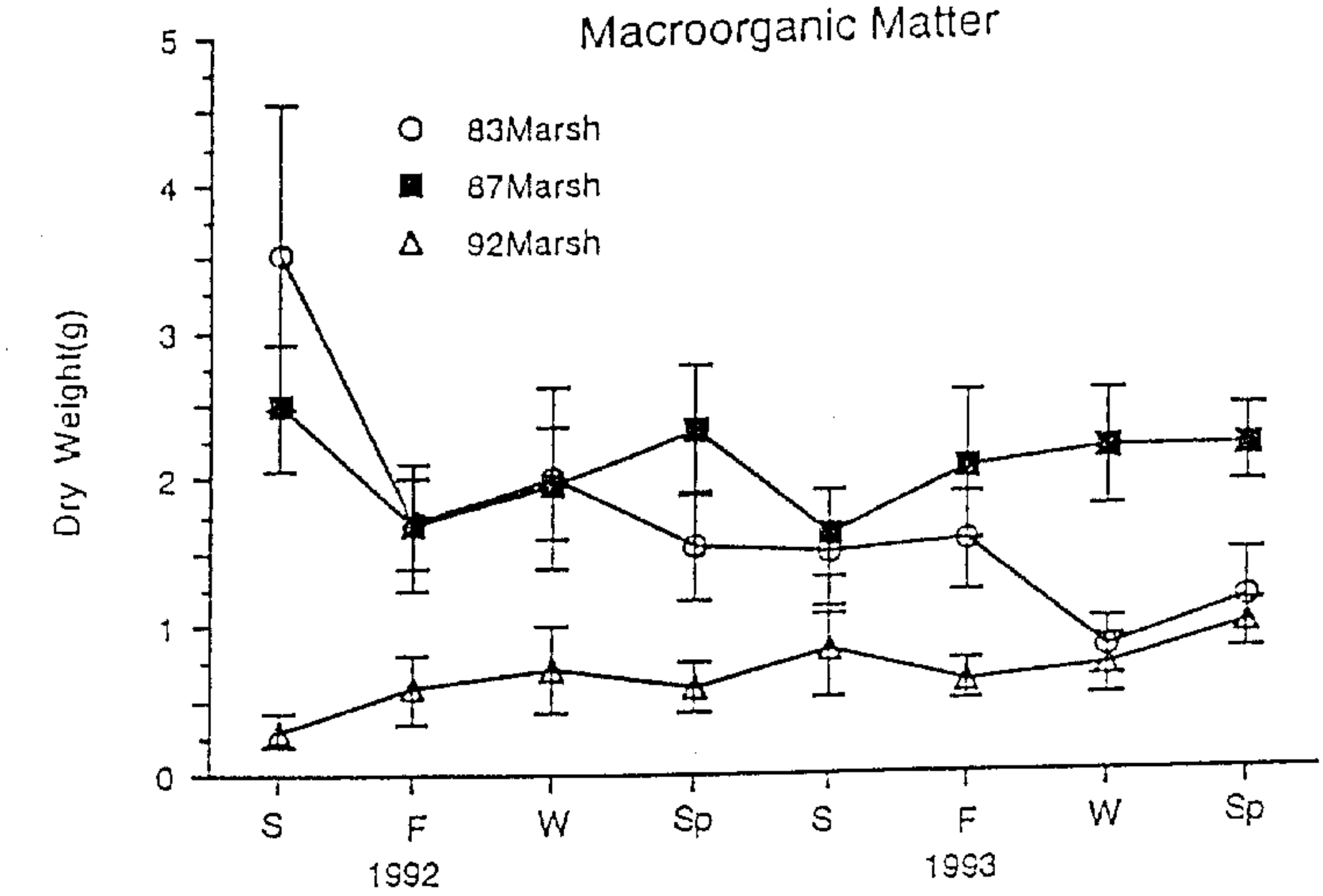


Fig. 6. Trophic structure within the polychaetes at each created salt marsh. The dominant polychaete species were assigned to feeding groups (see Table 1) that included carnivores (C), omnivores (O), surface-deposit feeders (SDF, subsurface deposit feeders (SsDF), and suspension feeders (SuF). Pie sections represent the relative abundance of each trophic group over the 2-year study period.

retained on the 0.5-mm sieve) in sediments was consistently lower in the 92Marsh than in the other two marshes (Fig. 7). MOM in the 92Marsh appeared to increase over the 2-year study period, and during the last two sampling periods there was no significant difference between MOM in the 92Marsh and the 83Marsh (Table 2). In part, however, this change occurred because MOM in the 83Marsh declined over the study. In comparison, MOM in the 87Marsh was relatively stable over the study period and was significantly higher than MOM in the 92Marsh for seven of the eight sampling periods. Elevated MOM values in the 83Marsh and 87Marsh during the first sampling period were due to high values for live roots and rhizomes associated with *Spartina* stems. The percentage of MOM made up by live roots and rhizomes in the 83Marsh and 87Marsh ranged between 50% and 70% during six of the eight seasonal sampling periods (Fig. 7). However, live roots and rhizomes made up a significantly lower percentage of MOM in the 92Marsh for the first year of the study, and this percentage in the 92Marsh increased over the 2-year sampling period. During the second year of the study, the percentage of live MOM was more stable and similar among the three marshes; therefore, differences among the marshes for both the



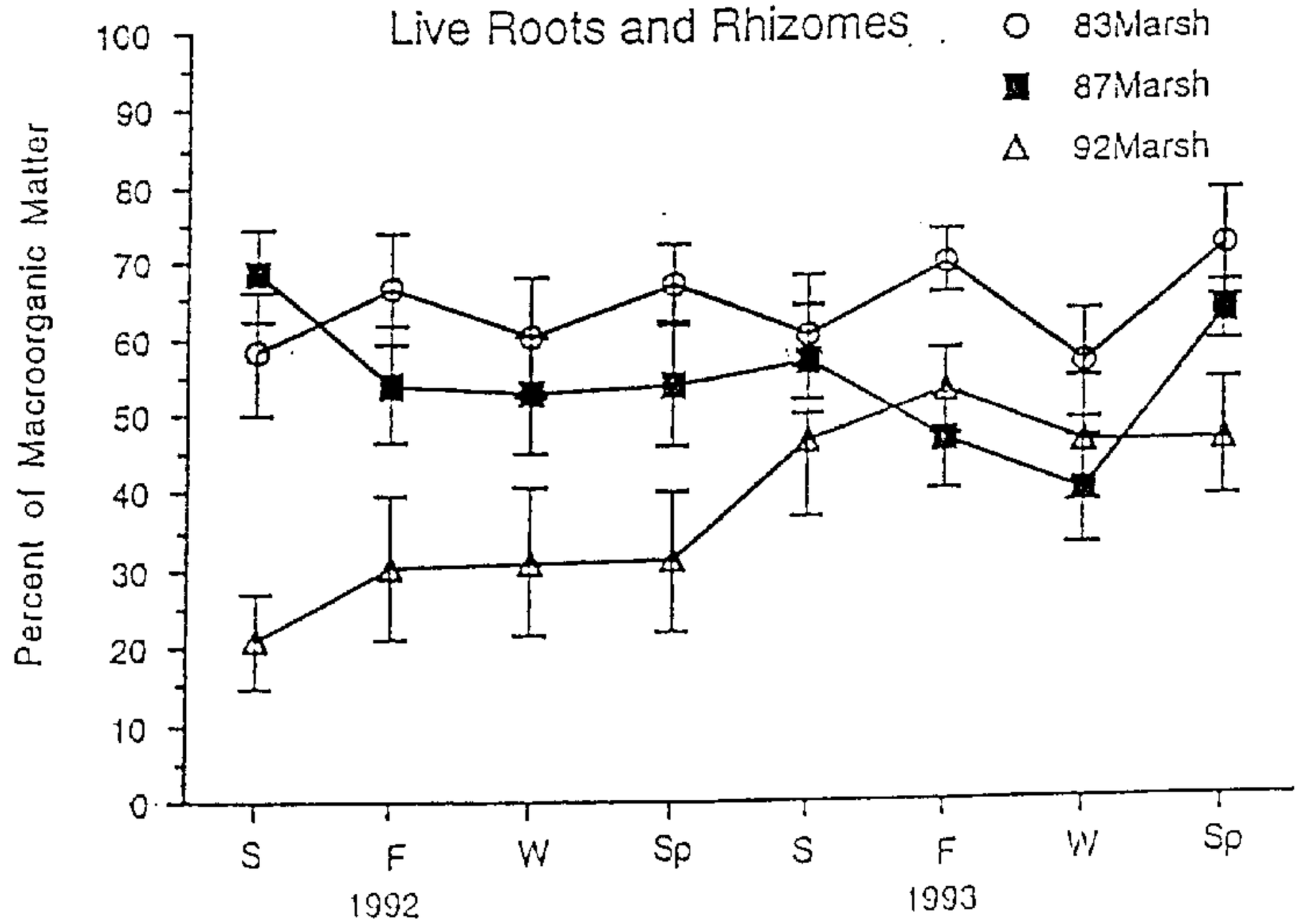


Fig. 7. Mean (+/- 1 SE) dry weight of macroorganic matter (from 78.5-cm² sediment cores) and the percent live roots and rhizomes within the macroorganic matter at the three created marshes on Pelican Spit for the eight seasonal sampling periods.

live and dead components of MOM were similar to the patterns apparent for total MOM (Fig. 7).

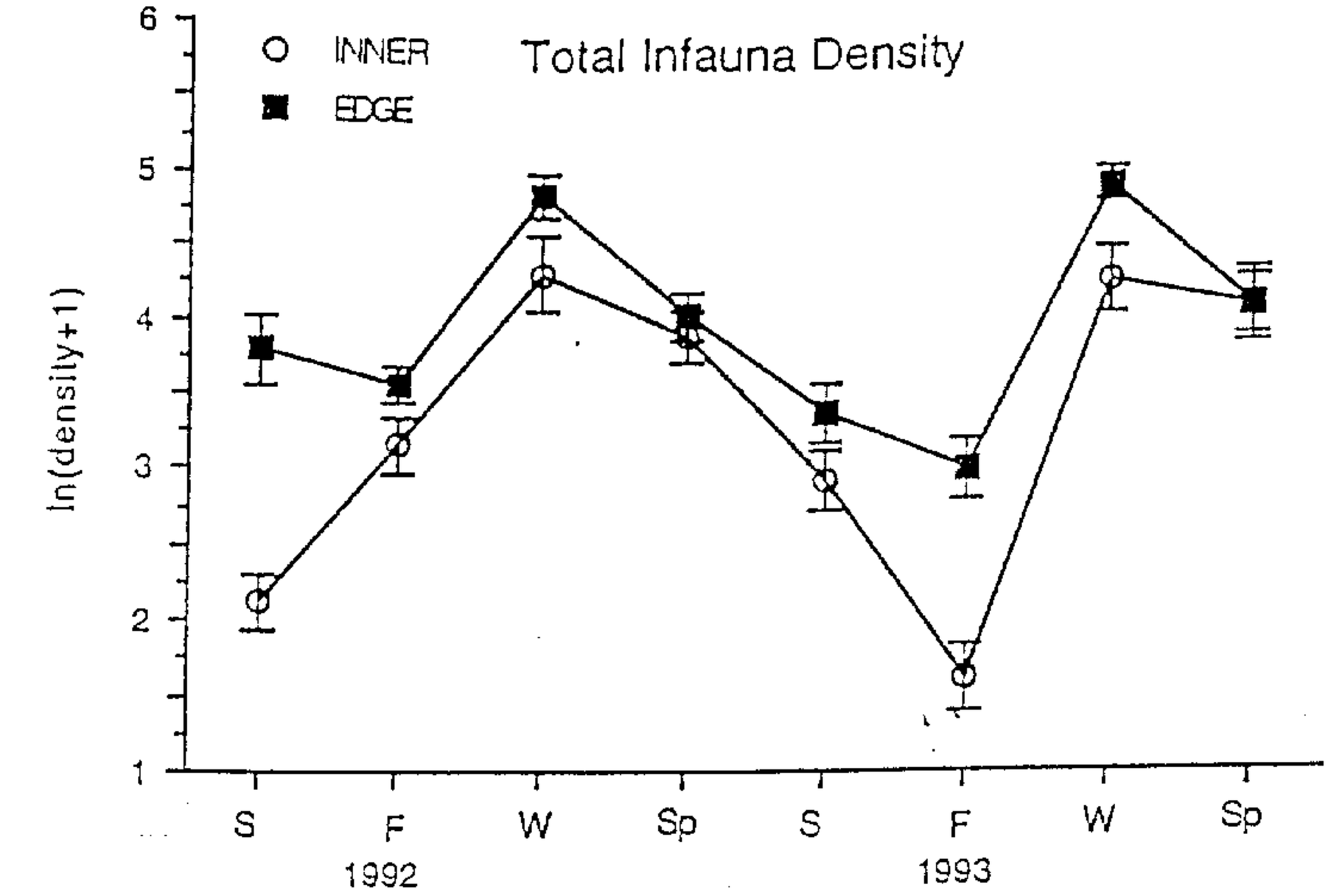
Sediment grain size was analyzed for fall and winter 1993 samples. Patterns among the marshes were similar for these two sampling periods, and the data were combined for statistical analyses. The percentage of sand, silt, and clay were measured. Sediments from all three marshes were predominantly composed of sand-sized particles, and included very little silt. The percent clay did vary among the marshes, and was analyzed in detail. On the basis of ANOVA contrasts, the overall percent of clay in the 92Marsh (13.1%, SE = 0.91) was not significantly different from the percent in the 83Marsh (8.6%, SE = 0.85), but the 92Marsh was significantly different from the 87Marsh (22.7% sand, SE = 3.69). However, there was a strong interaction between Elevation and Marsh in the data (ANOVA p value < 0.001); and at the marsh edge, the percent of clay was similar among all marshes, ranging from 7.8% to 13.7%. In the inner marsh, ANOVA contrasts indicated that the percent of clay in the 87Marsh (37.6%, SE = 4.87) was significantly higher than at both the 83Marsh (8.32%, SE = 0.48) and the 92Marsh (12.5%, SE = 1.19).

Marsh Surface Elevation

Total infaunal abundance was significantly higher in edge habitat compared with inner marsh habitat during six of the eight sampling periods (Fig. 8; main effect of Elevation, Table 2). Biomass was significantly higher in edge habitat during two of the eight periods. There were significant interactions between Marsh and Elevation in the ANOVAs for both total infaunal abundance and biomass (Table 2), but the general pattern of no consistent differences among marshes seen in the combined data (Fig. 3) was apparent at both elevations.

Streblospio benedicti was also generally more abundant in the edge habitat, but differences among marshes varied with elevation for this species (Fig. 9). In the inner marsh habitat, there were no consistent differences among the three created marshes. In edge habitat, however, the abundance of *S. benedicti* in the 92Marsh was lower than in the older marshes for seven of the eight significant contrasts (Marsh versus Elevation interaction, Table 2).

Capitella capitata was consistently more abundant in the inner marsh habitat, and this difference was significant during five of the eight sampling periods (main effect of Elevation, Table 2). The pattern of



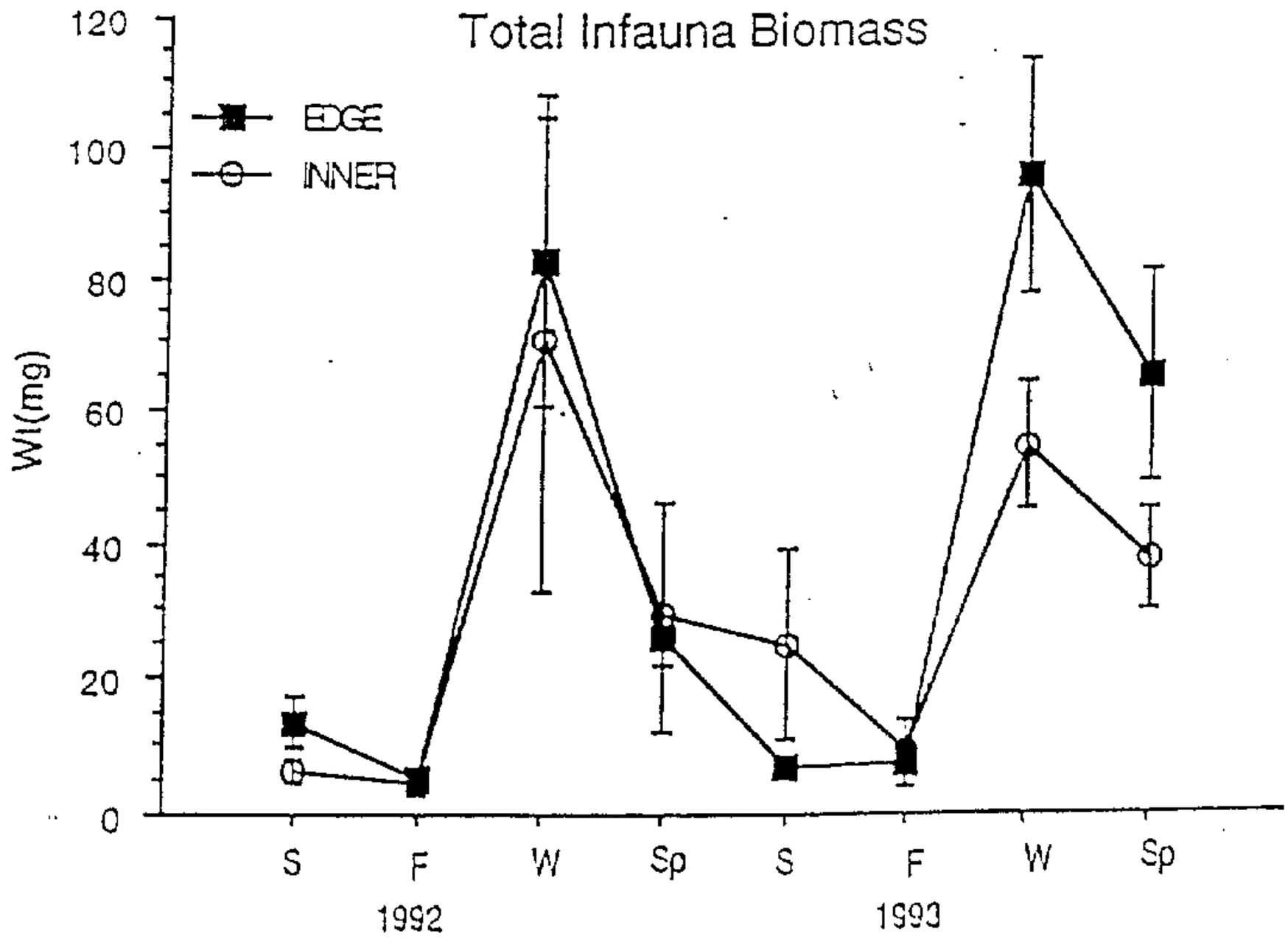


Fig. 8. Mean (+/- 1 SE) density (ln transformed) and biomass of total infauna along the inner and edge transects for the eight seasonal sampling periods. Values are from 78.5-cm² sediment cores, and data are combined from the three created marshes.

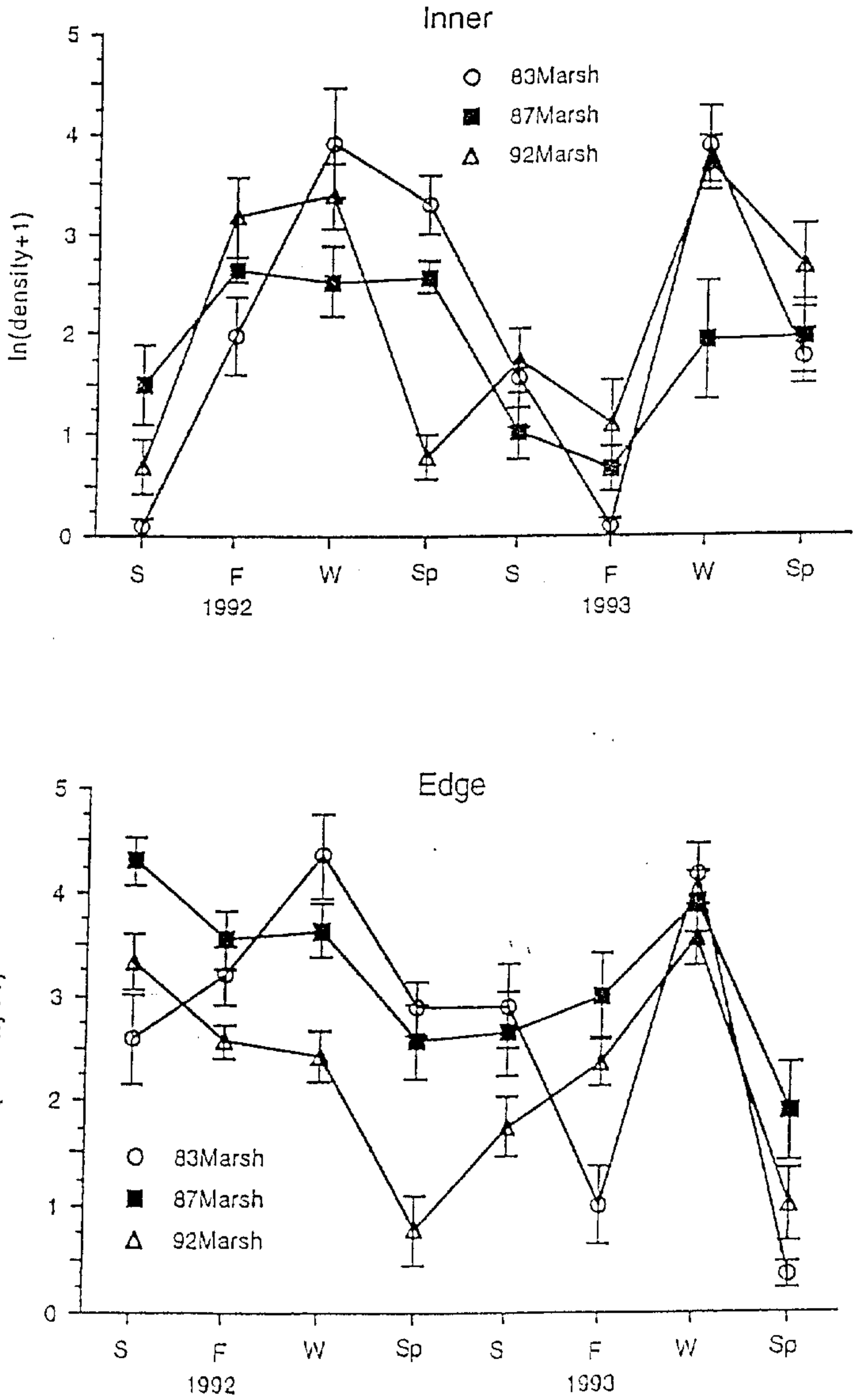


Fig. 9. Mean (+/- 1 SE) density (ln transformed) of *Streblospio benedicti* along the inner and edge transects of the three created marshes during the eight seasonal sampling periods. Values are from 78.5-cm² sediment cores.

differences among marshes varied with elevation for this species, and the Marsh versus Elevation interaction in the ANOVA was significant for six of the eight sampling periods (Table 2). In the edge habitat, densities in the 92Marsh were only significantly different from the older two marshes in four of 16 contrasts (Fig. 10; Table 2); in each of these comparisons, densities in the 92Marsh were higher than in the older marshes. In the inner marsh, the abundance of *C. capitata* was frequently different among marshes; and in all 11 significant contrasts, the densities in the 92Marsh were higher than in the other marshes.

Crustaceans were generally more abundant in the edge habitat, and this difference was most pronounced during the winter and spring (Fig. 11). Comparisons of the three marshes at each elevation were similar to the overall marsh comparison (Fig. 5), and the Marsh versus Elevation interaction was seldom significant in the ANOVAs (Table 2).

Sediment organic content was significantly higher in the inner marsh compared with edge habitat during seven of the eight sampling periods (Fig. 11; main effect of Elevation, Table 2). Differences in SOC among the three marshes were mainly due to differences in SOC levels in

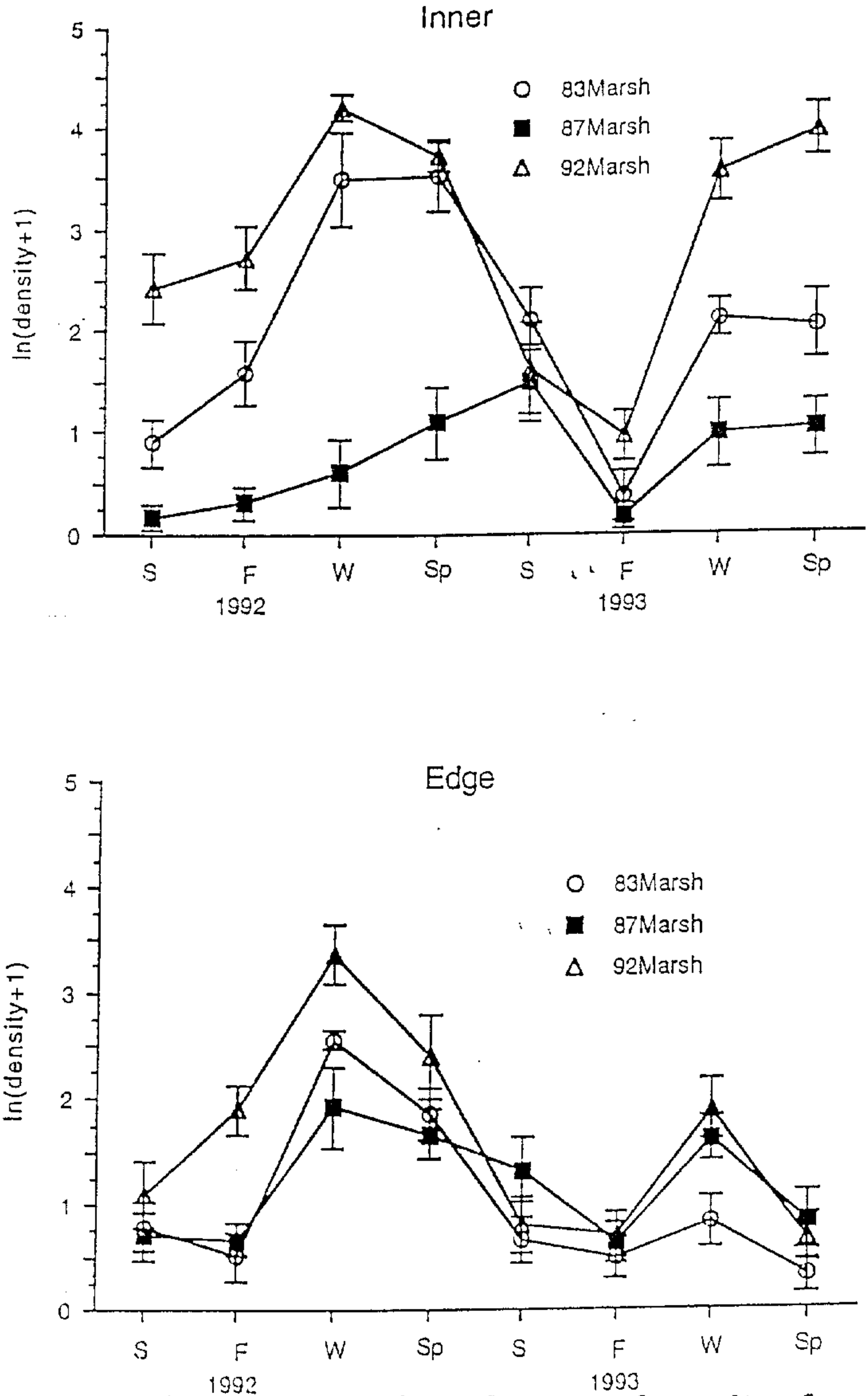


Fig. 10. Mean (+/- 1 SE) density (ln transformed) of *Capitella capitata* along the inner and edge transects of the three created marshes during the eight seasonal sampling periods. Values are from 78.5-cm^2 sediment cores.

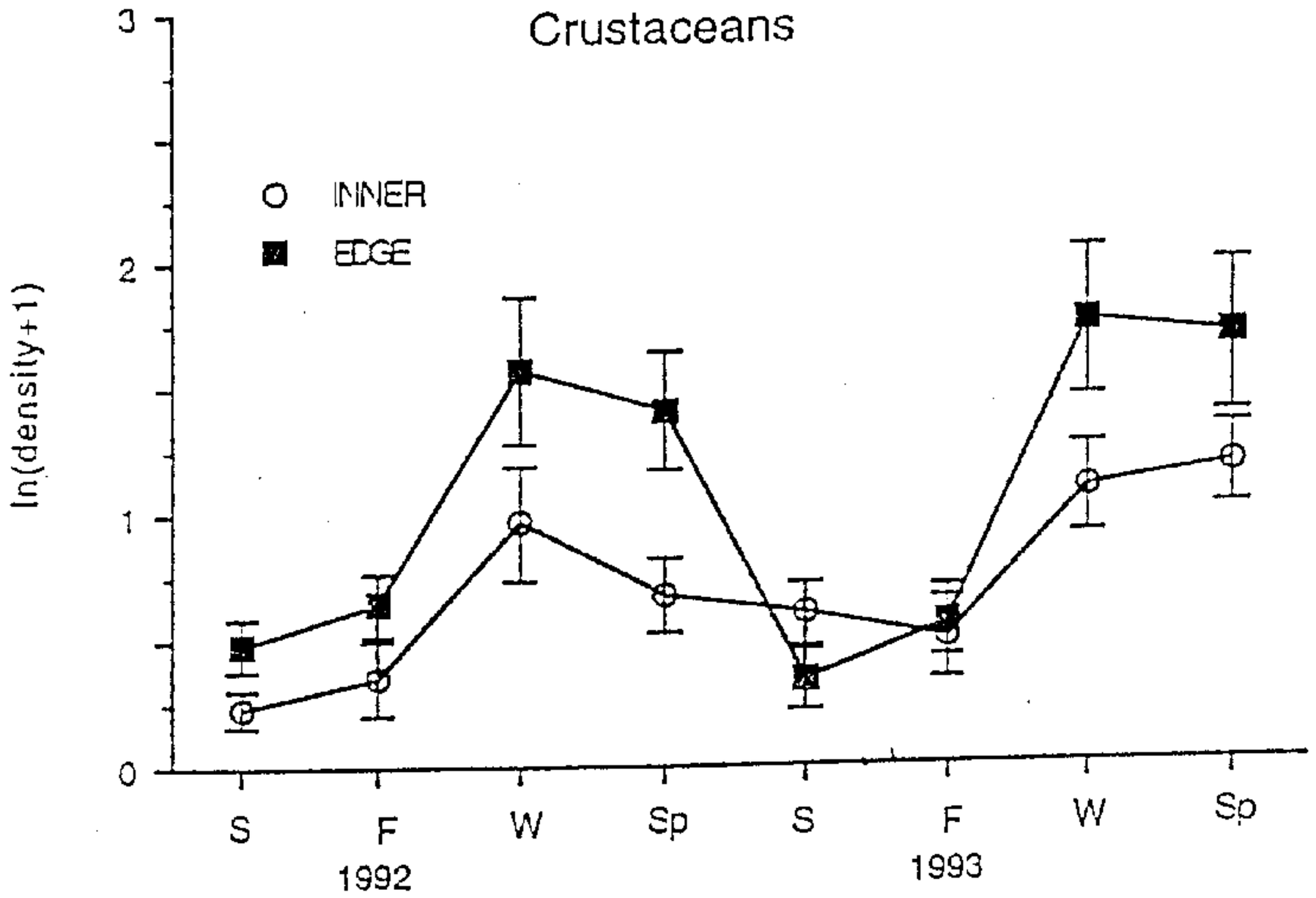


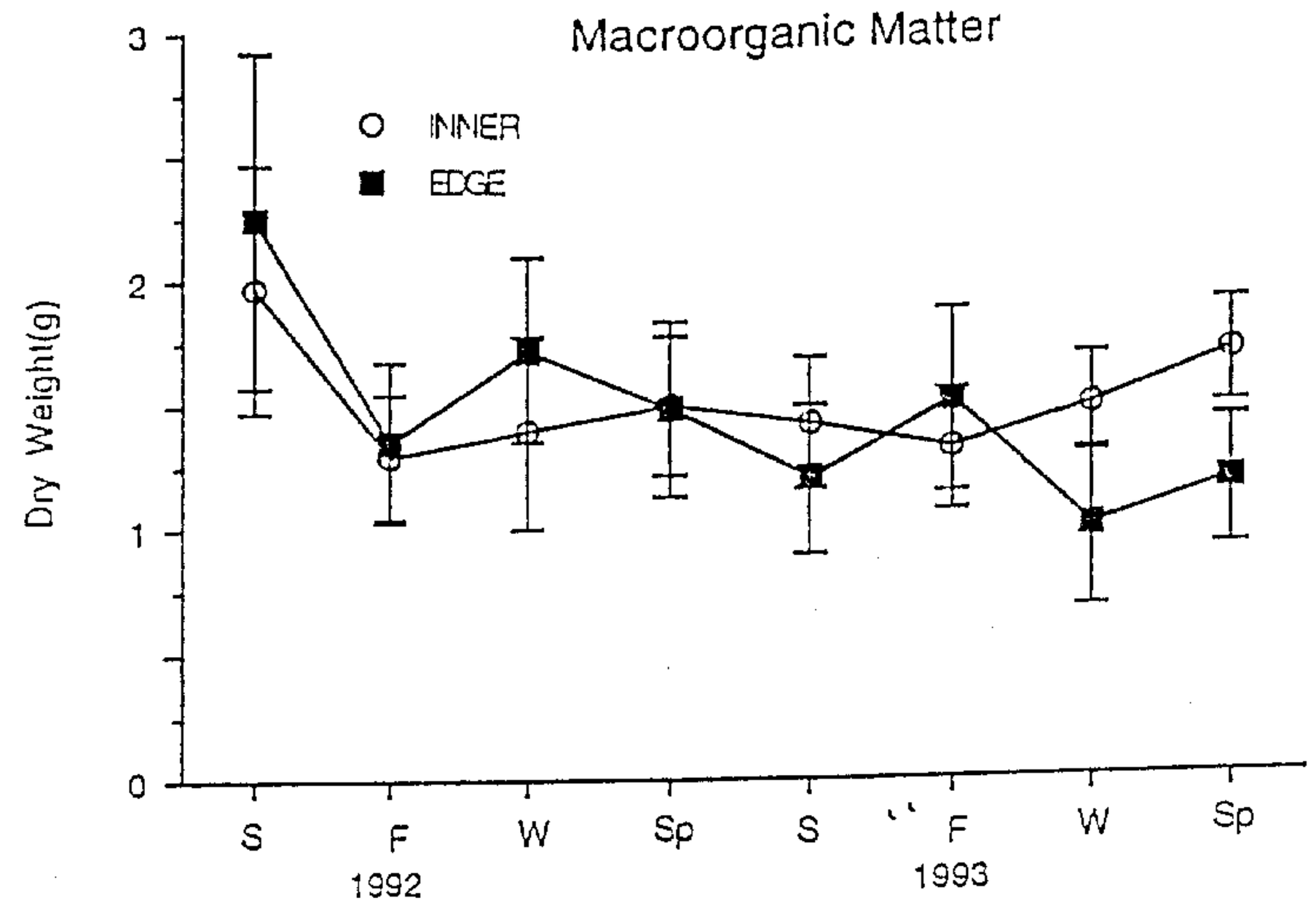
Fig. 11. Mean density (ln transformed +/- 1 SE) of total crustaceans and the sediment organic content (% dry weight lost on ignition) along the inner and edge transects for the eight seasonal sampling periods.

the inner transects of the three marshes. In edge habitat, there were no significant differences in SOC between the 92Marsh and the other marshes (contrasts within the Marsh versus Elevation interaction, Table 2). In the inner marsh, however, the distribution of SOC among the marshes was similar to that shown in Fig. 5; and SOC at the 87Marsh was significantly higher than at the 92Marsh during seven of the eight sampling periods.

Macroorganic matter in the sediment cores varied little between elevations (Fig. 12), although values were significantly higher in the inner marsh during the last two sampling periods (main effect of Elevation, Table 2). MOM levels were highest in the 87Marsh and lowest in the 92Marsh (Fig. 7) at both elevations. Although the mean percentage of live roots and rhizomes was generally highest in the edge habitat (Fig. 12), this difference was only significant during one sampling period (Table 2).

Proximity to *Spartina* Stems

Total infaunal abundance and biomass were generally higher in samples taken near *Spartina* stems (Fig. 13), and the main effect of this proximity was significant in ANOVAs during seven sampling periods for abundance and four sampling periods for biomass (Table 2). Although



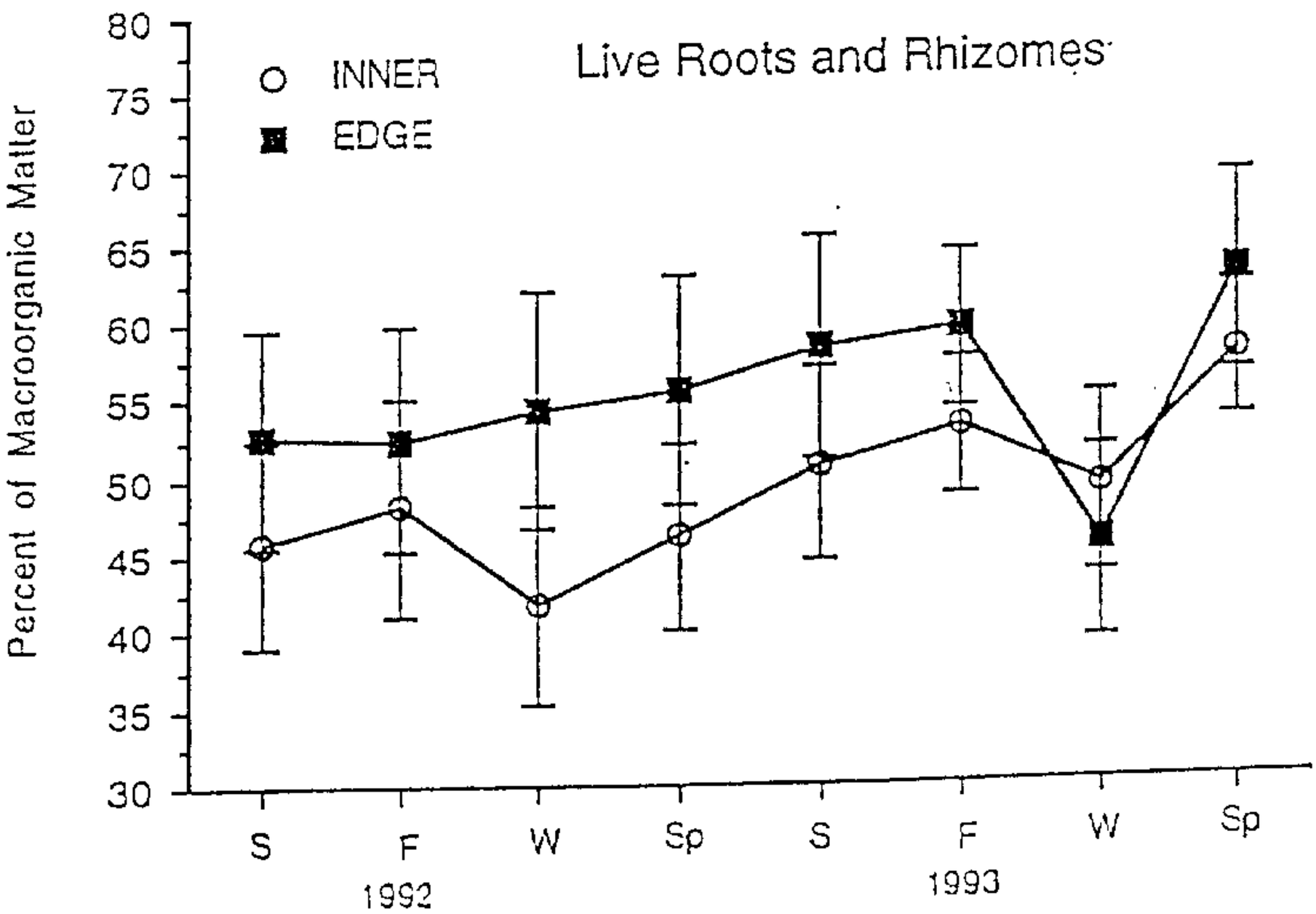


Fig. 12. Mean dry weight (+/- 1 SE) of macroorganic matter and the percent of live roots and rhizomes within the macroorganic matter along the inner and edge transects for the eight seasonal sampling periods.

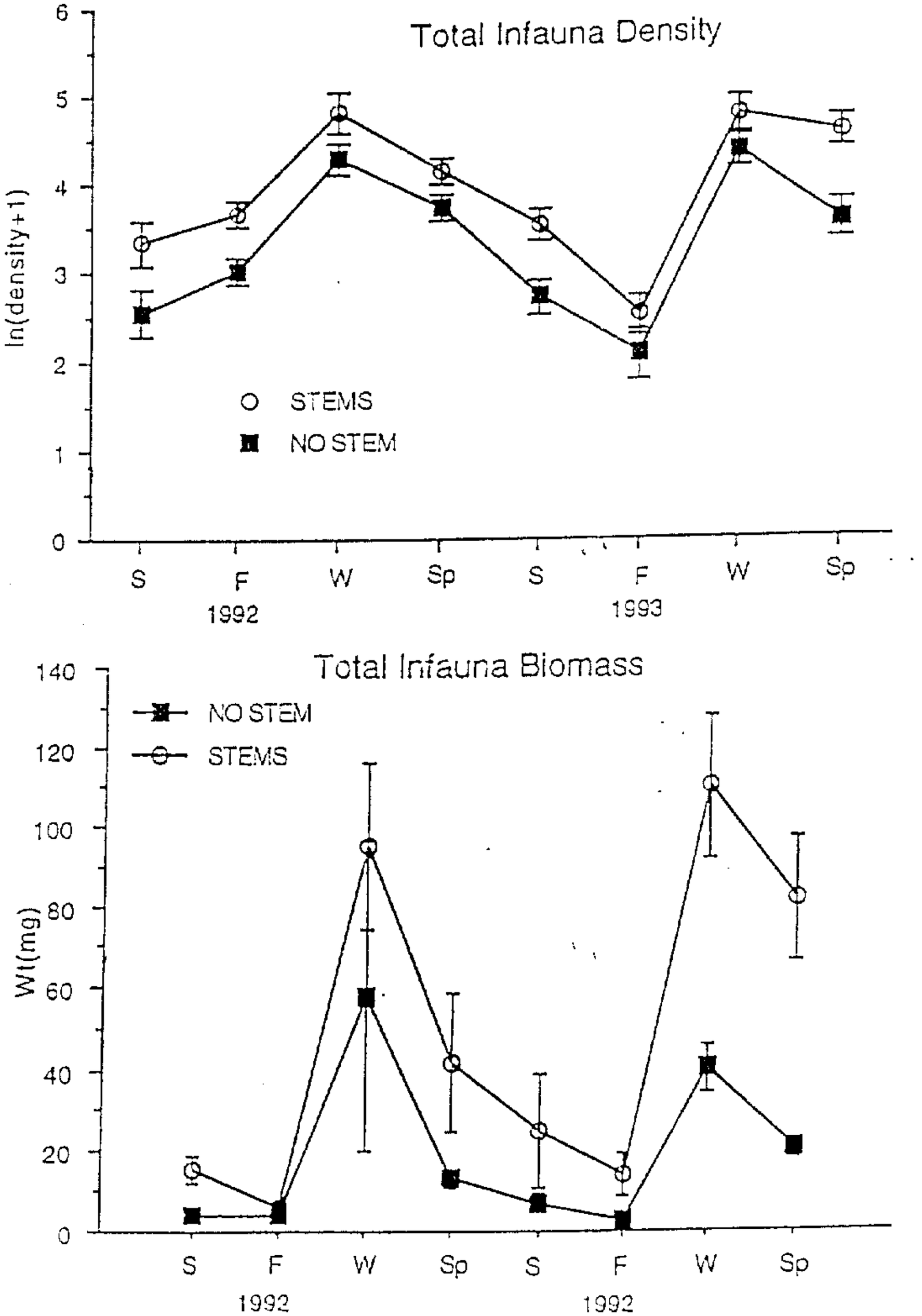
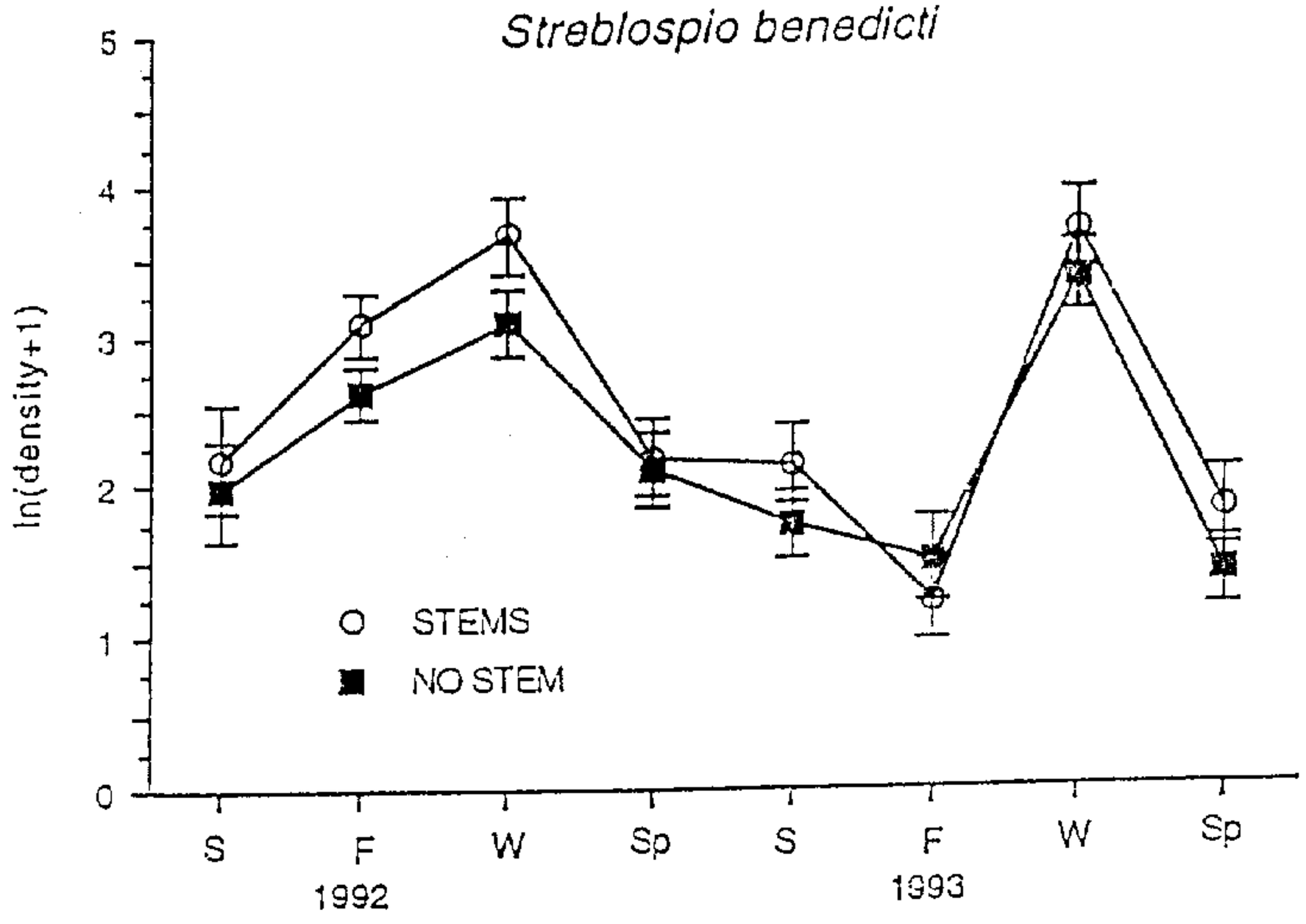


Fig. 13. Mean (+/- 1 SE) density (ln transformed) and biomass of total infauna near and between the stems of *Spartina alterniflora* during the eight seasonal sampling periods. Values are from 78.5-cm^2 sediment cores, and data are combined from the three created marshes.

mean abundances of the two dominant polychaetes *Streblospio benedicti* and *Capitella capitata* were consistently higher near stems (Fig. 14), the difference was relatively small and generally not statistically significant (main effect of Proximity, Table 2). Crustaceans, however, were much more abundant near *Spartina* stems (Fig. 15), and the difference was significant during fall, winter, and spring (Table 2). There was no significant effect of Proximity during summer sampling periods when crustacean abundances were low. Over 90% of all crustaceans were collected near *Spartina* stems, and this pattern was apparent for all abundant species within the group. Sediment organic content did not vary with proximity to *Spartina* stems (Fig. 15; Table 2), but the amount of macroorganic matter (roots, rhizomes, and detritus) and the percent of live roots and rhizomes were significantly higher near stems during every sampling period (Fig. 16; Table 2). Differences among the three marshes did not appear to vary in relation to stem proximity for any of the dependent variables examined, and there were few significant interactions between Marsh and Proximity in the ANOVAs (Table 2).



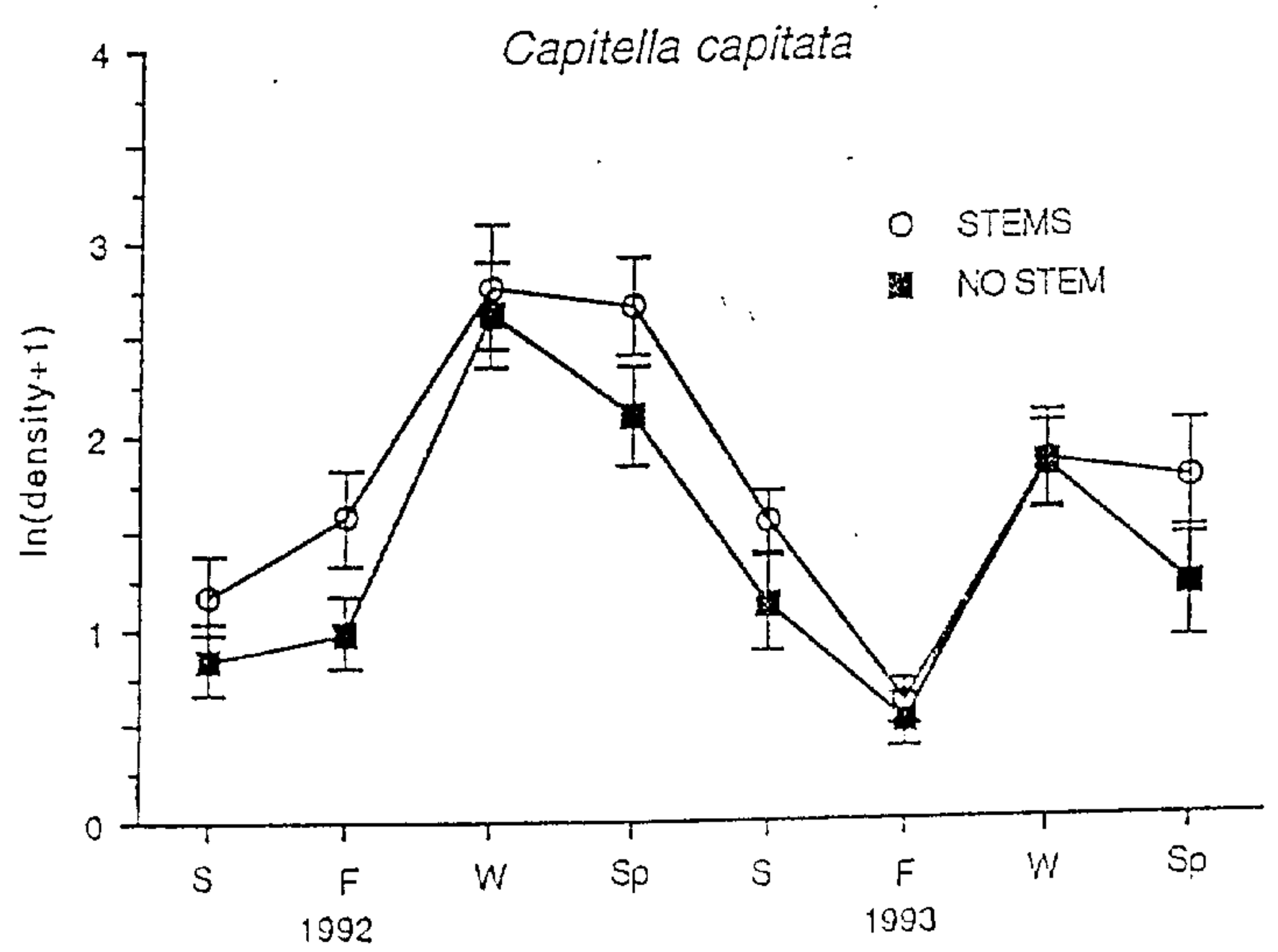


Fig. 14. Mean (+/- 1 SE) density (ln transformed) of the two dominant polychaete species near and between stems of *Spartina alterniflora for* the eight seasonal sampling periods. Values are from 78.5-cm² sediment cores, and data are combined from the three created marshes.

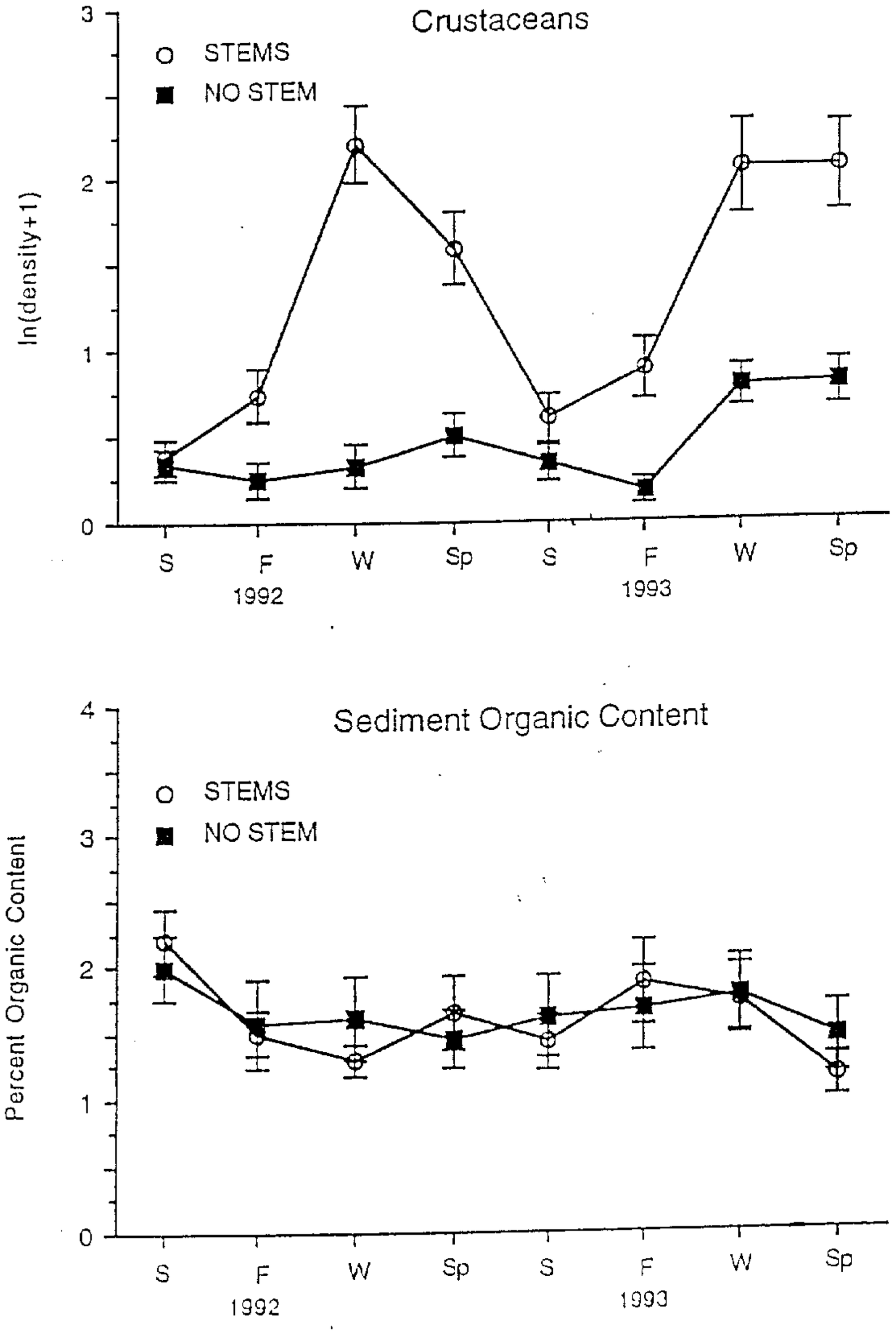


Fig. 15. Mean density (ln transformed +/- 1 SE) of total crustaceans and the sediment organic content (% dry weight lost on ignition) near and between stems of *Spartina alterniflora* for the eight seasonal sampling periods.

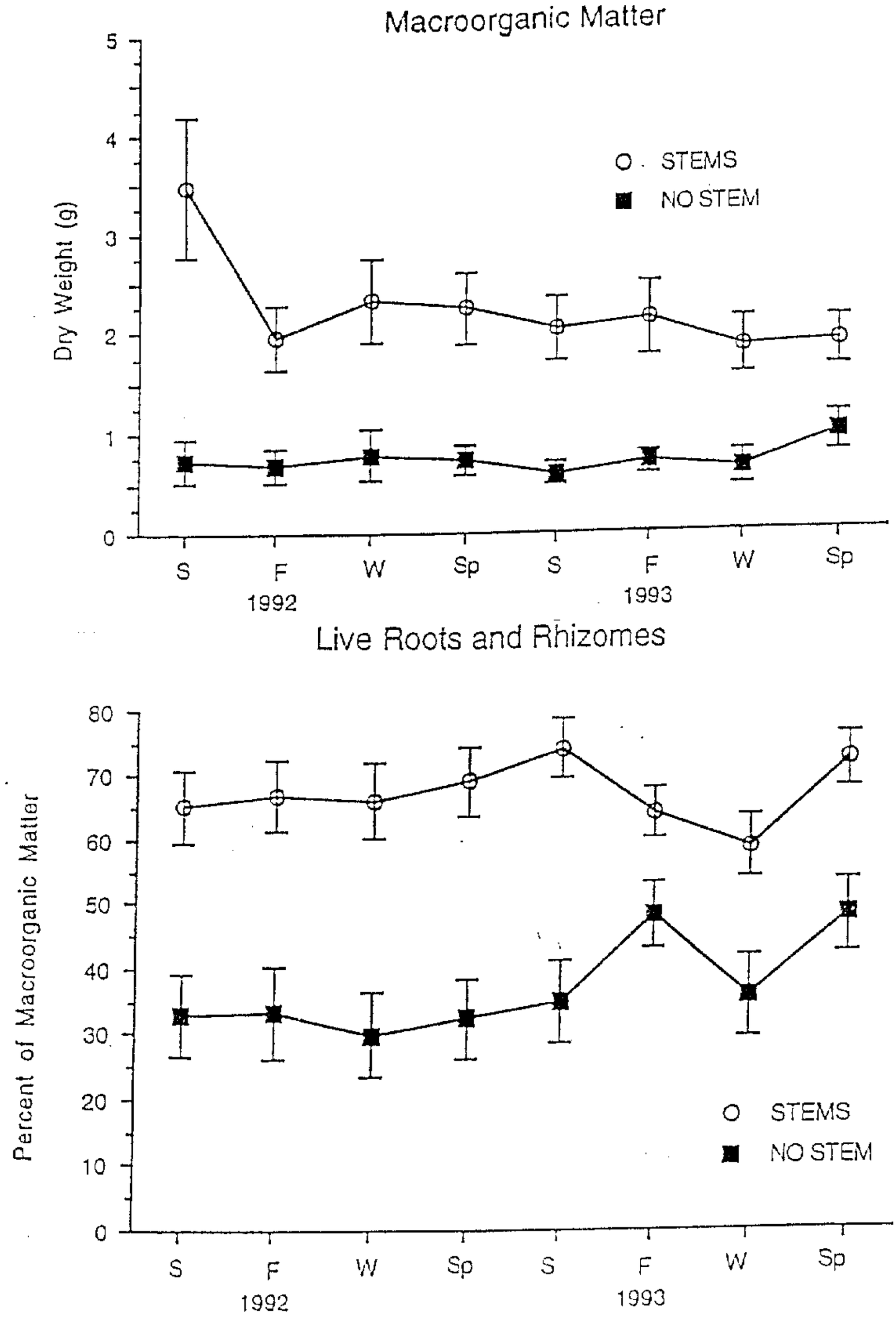


Fig. 16. Mean (+/- 1 SE) dry weight of macroorganic matter (from 78.5-cm^2 sediment cores) and the percent of live roots and rhizomes within the macroorganic matter both near and away from *Spartina alterniflora* stems during the eight seasonal sampling periods. Data are combined from the three created marshes.

Species Richness

Results indicate that the number of annelid (all polychaetes) species identified in the three marshes was similar in summer 1992, only 1 month following planting of the 92Marsh (Fig. 17). Species richness in this taxonomic group increased during the winter when abundances were high, but there was no evidence for differences among the three marshes. No crustaceans were collected in the 92Marsh during the first sampling period, but in subsequent sampling periods there did not appear to be any difference in species richness of crustaceans among the three marshes.

Comparison With Past Studies

Comparison of infauna and macroorganic matter in the 83Marsh and 87Marsh before and after creation of the 92Marsh indicated that infaunal abundance, species composition, trophic structure, and levels of macroorganic matter in the two older marshes did not change significantly with the creation of the 92Marsh (Fig. 18).

Comparison With Natural Marshes

When data from the 83Marsh and 87Marsh in 1990/1991 were compared with five nearby natural marshes, ANOVA results indicated that macroorganic matter was lower in

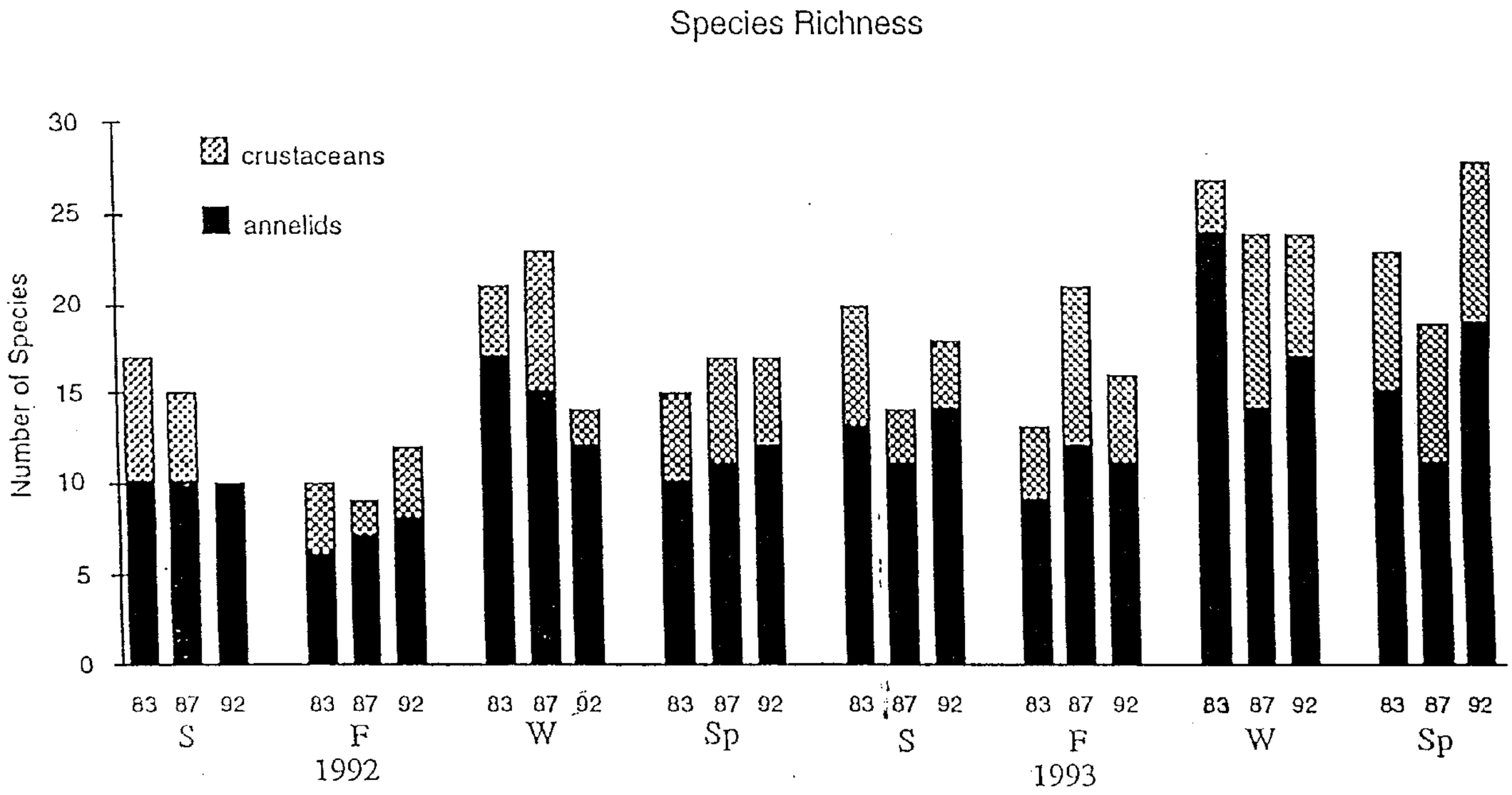
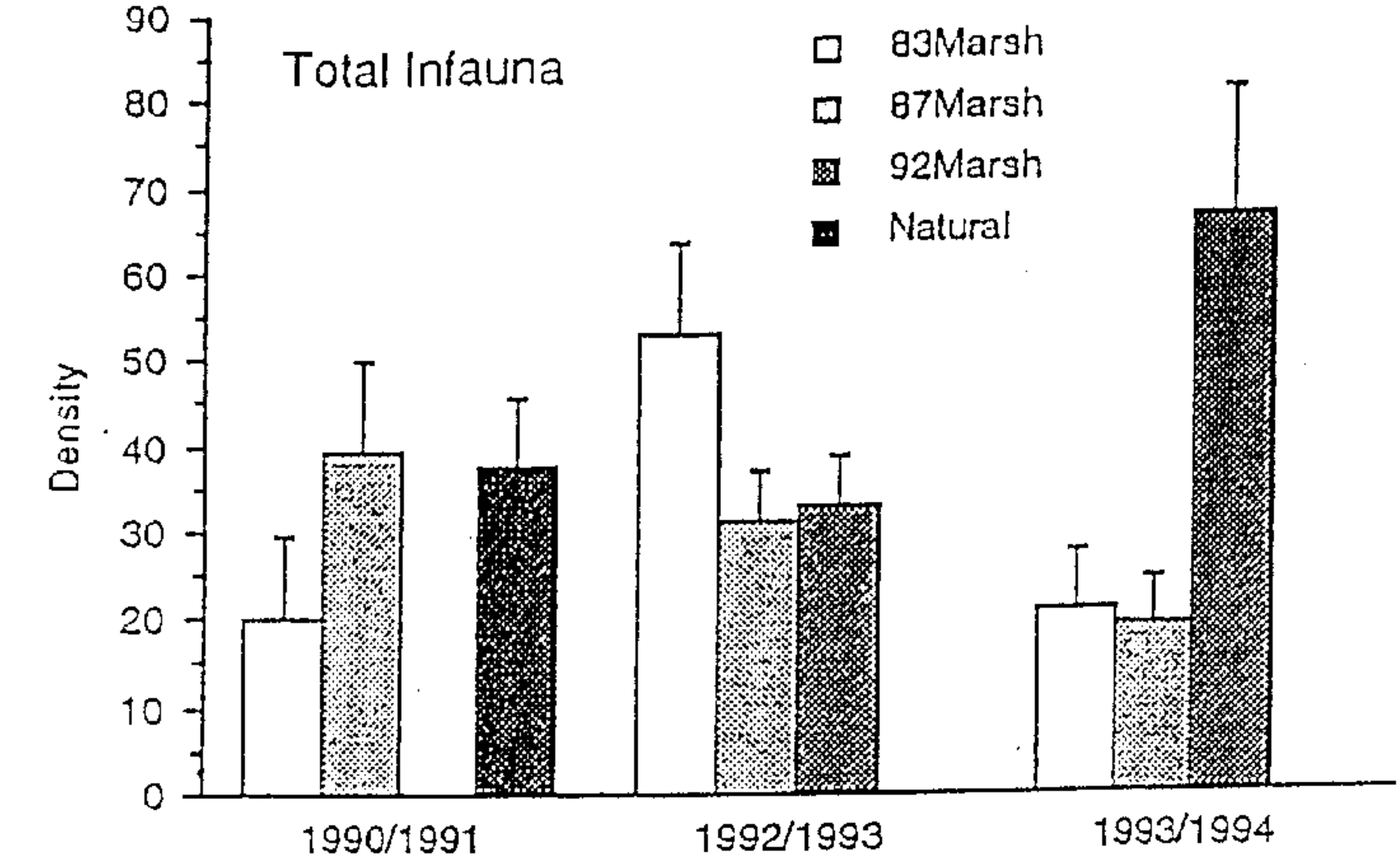


Fig. 17. Number of annelid and crustacean species in the three created salt marshes during the eight seasonal sampling periods.



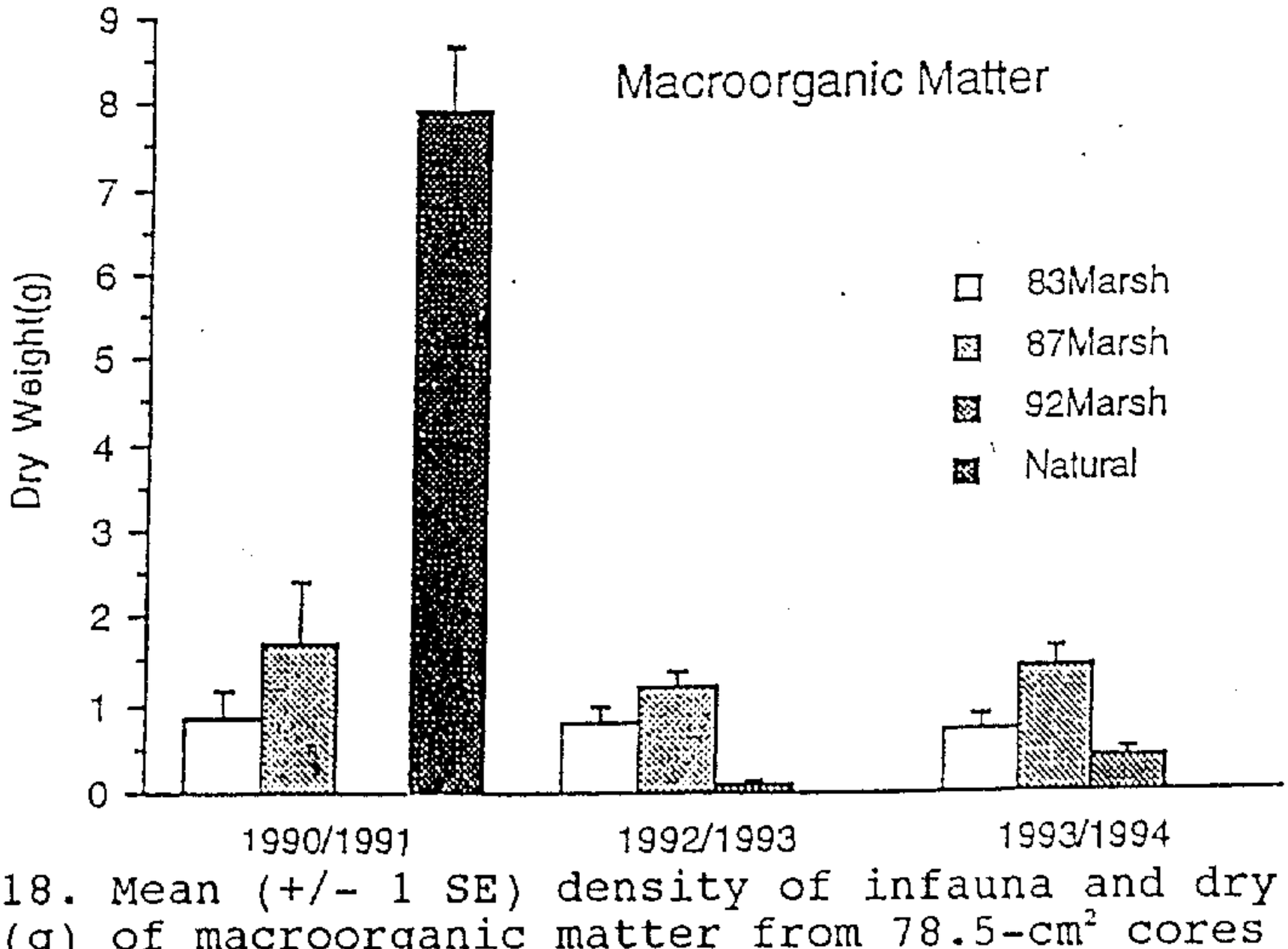


Fig. 18. Mean (+/- 1 SE) density of infauna and dry weight (g) of macroorganic matter from 78.5-cm^2 cores taken at the created salt marshes on Pelican Spit before and after the creation of the 92Marsh. Data from five natural marshes in the Galveston Bay system are also shown for the 1990/1991 year. Data are combined from the fall and spring (e.g., fall 1990 and spring 1991) and from inner and edge habitats. Only cores taken between *Spartina* stems were included in these means. Summer and winter data were not available for 1990/1991 and were therefore not included for other years.

the two created marshes at Pelican Spit than in the natural marsh. Most polychaetes in the two created marshes were surface deposit feeders. While surface deposit feeders were also abundant in the natural marshes, the natural marshes also supported greater numbers of carnivorous polychaetes (Fig. 19).

Regression Analysis

Relationships Among Independent Variables

Sediment organic content was expressed as percent by weight of organic matter lost from dry sediment. Values obtained by the digestion method were lower than those obtained by weight loss on ignition, but results of the two methods were highly correlated (Fig. 20). The wet-oxidation technique was used only on winter and spring 1993 samples. The mean %SOC using this technique was 0.87%, (SE= 0.08), with values ranging from 0.15% to 4.55%. The mean percent SOC as determined by weight loss on ignition was 1.50%, (SE=0.122), and values ranged from 0.37% to 6.91%.

Sediment grain size is expressed as percent clay, and was measured during the winter and fall 1993 sampling periods. The mean percent clay in the sediments was 14.78%, (SE=1.419). The percent clay was positively correlated with ASH during the winter and fall sampling

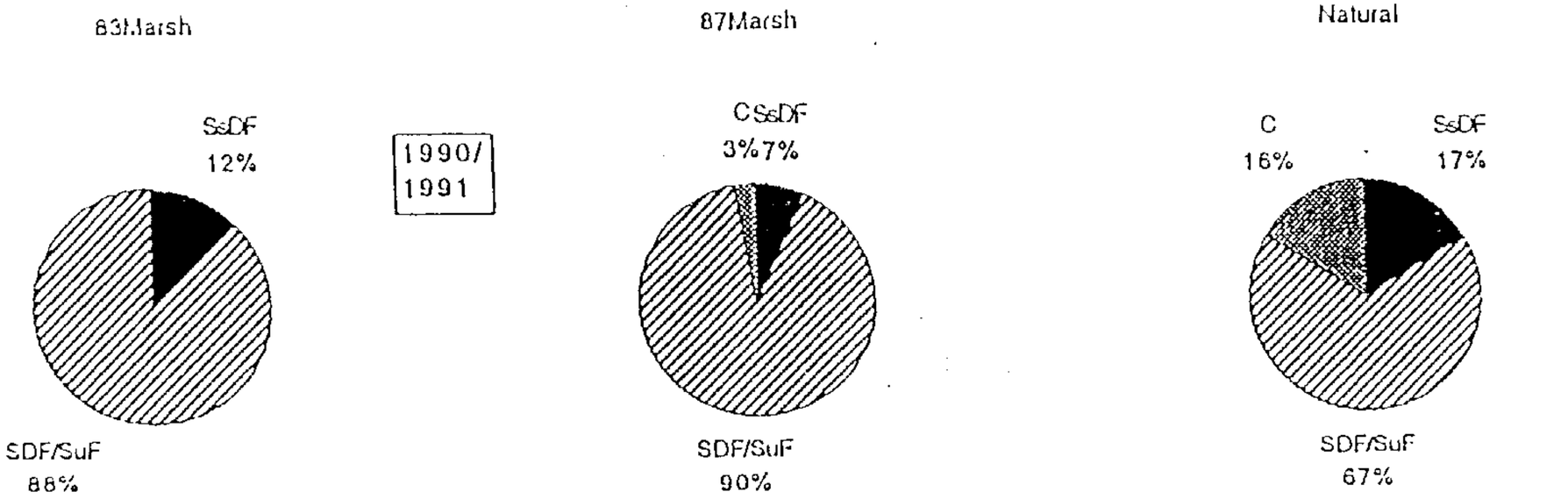


Fig. 19. Trophic relationships within the polychaetes at the 83Marsh, 87Marsh, and natural marshes during 1990/1991 (before creation of the 92Marsh) and at the 83Marsh, 87Marsh, and 92Marsh during 1992/1994 (the two years following creation of the 92Marsh). Only samples taken between *Spartina* stems taken in the fall and spring seasons are included in this analysis. Polychaete species were assigned to trophic groups including subsurface deposit feeders (SsDF), surface deposit feeders and suspension feeders (SDF/SuF), and carnivores (C) according to Gaston and Nasci (1988).

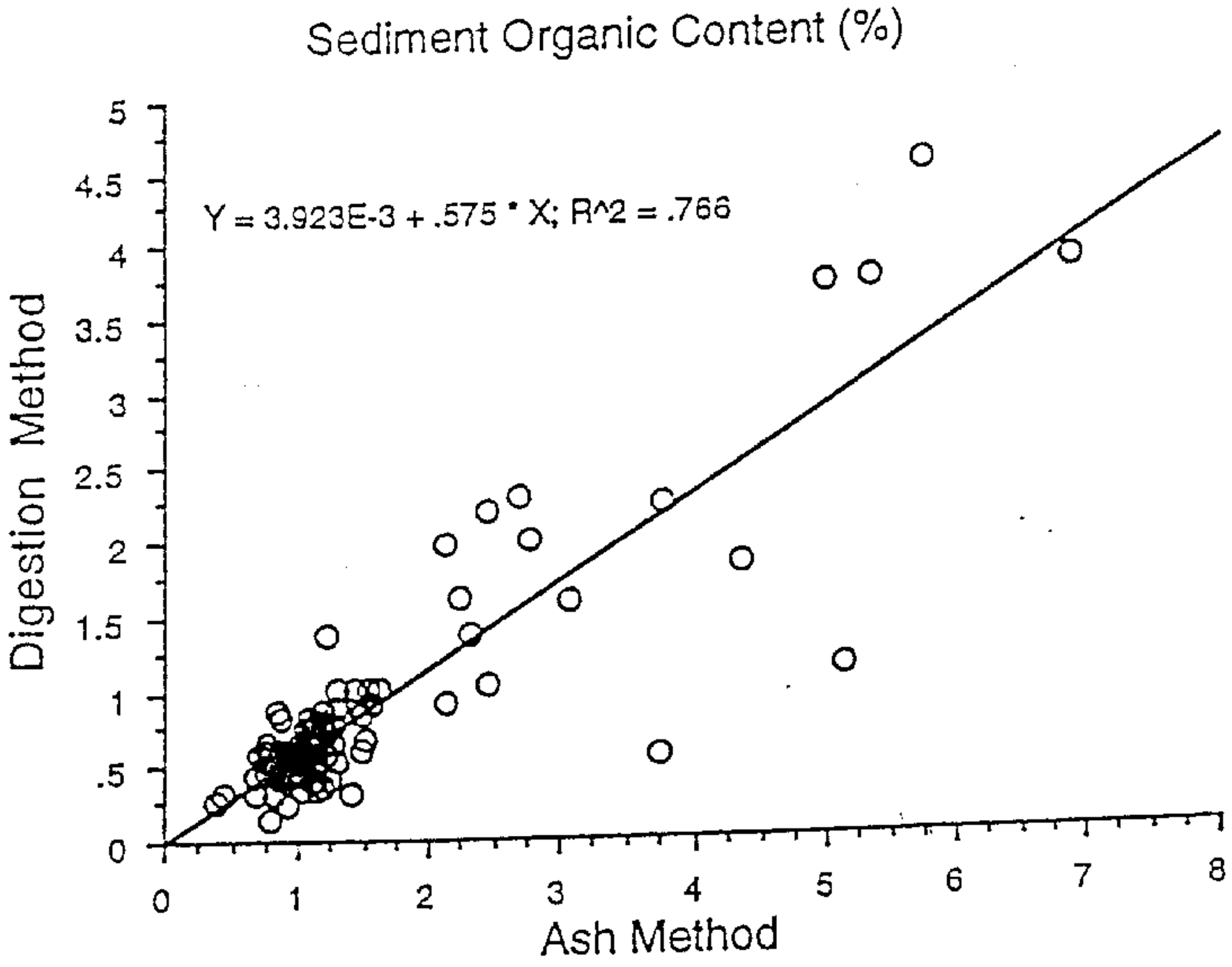


Fig. 20. Plot of the relationship between the results of the two procedures for measuring sediment organic content. Includes data from the winter and spring sampling periods of 1993 (n=96). Samples were from all three marshes, including both inner and edge transects, and both near and between stems. Top and bottom 2.5-cm sections are combined.

periods, with R^2 values of 0.352 and 0.659, respectively, and was also positively correlated with DIG during winter, when the R^2 value was 0.254 (Table 3).

The amounts of live (LMOM) and dead (DMOM) macroorganic matter in the cores were positively correlated with each other during the fall 1993 sampling period, and when the eight sampling periods were combined by season the relationship was significant during the summer, winter, and spring seasons (Table 3). LMOM was never correlated with the amount of sediment organic content (ASH) in the samples (Table 3). A positive relationship existed between the amount of dead macroorganic matter (DMOM) and ASH during each of the four seasons, with R^2 values ranging from 0.163 to 0.434 (Table 3).

Relationships With Infauna

Stepwise regression models were used to identify relationships between infaunal densities and ASH, LMOM, and DMOM for each season. In this analysis, data from the two annual sampling periods conducted during each season were combined. There was a consistent positive relationship between total infaunal abundance and the dry weight of LMOM; (Table 4). The relationship was significant during three of the four seasons. During

TABLE 3. R-squared values for relationships among the variables; sediment organic content determined by weight loss on ignition (ASH), weight of live roots and rhizomes (LMOM), weight of detrital matter (DMOM), sediment organic content determined by digestion (DIG), and percent clay-sized particles in the sediment (CLAY). NS indicates no statistically significant relationship where $p>0.05$. Data for seasons includes two sampling periods combined (n=96). Data for single sampling periods include 48 samples each.

Winter 1993

	DMCM	ASH	DIG	CLAY
LMOM	NS	NS	NS	NS
DMCM		NS	NS	NS
ASH			0.669	0.352
DIG				0.254

Spring 1993

	DMCM	ASH	DIG
LMCM	NS	NS	NS
DMCM		0.525	0.546
ASH			0.86

Fall 93

	DMCM	ASH	CLAY
LMOM	0.081	NS	NS
DMCM		0.349	0.371
ASH			0.659

SUMMER

	DMCM	ASH
LMOM	0.127	NS
DMCM		0.205

FALL

	DMCM	ASH
LMOM	NS	NS
DMCM		0.18

WINTER

	DMCM	ASH
LMOM	0.032	NS
DMCM		0.163

SPRING

	DMCM	ASH
LMOM	0.033	NS
DMCM		0.434

TABLE 4. Stepwise regression analysis on ln(x+1) transformed abundances of infauna using three independent variables; sediment organic content as determined by weight loss on ignition (ASH), live roots and rhizomes (LMOM), and dead roots and rhizomes and other detritus (DMOM). The independent variable name is shown in italics if the relationship is negative. Data for the four seasons include all samples (top and bottom 2.5-cm sections combined) taken in all three marshes during that season over the two year span of the study (n=96).

	Independent variable				
	Step 1	R2	Final		R2
Summer					
Total Infauna	*ASH*	0.079	*ASH*	LMOM	0.118
Streblospio benedicti			*ASH*		0.042
Capitella capitata			NS		
Tharyx marioni			*ASH*		0.068
Crustaceans			DMOM		0.056
Infaunal wt. (mg)			NS		
Fall					
Total Infauna	LMOM	0.090	LMOM	*DMOM*	0.139
Streblospio benedicti	*DMOM*	0.039	*DMOM*	LMOM	0.089
Capitella capitata			NS		
Tharyx marioni			NS		
Crustaceans			LMOM		0.104
Infaunal wt. (mg)			NS		
Winter					
Total Infauna			*ASH*		0.269
Streblospio benedicti			*ASH*		0.067
Capitella capitata			*ASH*		0.141
Tharyx marioni	*ASH*	0.156	*ASH*	*LMOM*	0.199
Crustaceans			LMOM		0.097
Infaunal wt. (mg)			NS		
Spring					
Total Infauna	*ASH*	0.107	*ASH*	LMOM	0.176
Streblospio benedicti	DMOM	0.130	DMOM	LMOM	0.177
Capitella capitata			NS		
Tharyx marioni			*DMOM*		0.201
Crustaceans	LMOM	0.127	LMOM	*ASH*	0.166
Infaunal wt. (mg)			LMOM		0.090

some seasons, positive relationships with LMOM were also observed for densities of crustaceans and *S. benedicti*, and biomass of total infauna. A significant negative relationship between ASH and total infaunal abundance was evident during three of the four seasons. This negative relationship also occurred between ASH and densities of crustaceans, *S. benedicti* and *C. capitata*.

When regression analyses for each season were run separately for each of the three marshes, it was apparent that the negative relationship between total infaunal abundance and ASH existed only in the 87Marsh, where the inner transect consistently had high sediment organic values (Figs. 5 and 11). In the 87Marsh, abundances of total infauna, *S. benedicti* and *C. capitata* were low in the inner transect, and the negative relationship between their abundance and ASH was relatively strong (R2 values between 0.105 and 0.345). ASH appeared to be most strongly related to infaunal abundance during the winter.

DISCUSSION

In determining whether created marshes function similarly to natural marshes, evidence has been found that created marshes do not support similar levels of fauna (Moy and Levin 1991; Minello and Zimmerman 1992; Scattolini and Zedler 1996). Complex interactions within marshes and limited knowledge of linkages between marshes and estuaries have been cited as reasons for the low level of predictability concerning created marshes (Moy and Levin 1991). If created marshes are unsuccessful at providing infaunal food for fishery species, then the factors controlling infaunal populations must be identified, and it must be determined whether created marshes will better approximate natural marsh function with increasing age.

Patterns of Infaunal Distribution

The two older marshes on Pelican Spit were created five and nine years earlier than the newest marsh. Yet, within the first year of its existence, the 92Marsh was similar to the older marshes on the basis of total infaunal density, biomass, and species richness. Overall infauna density in the 92Marsh was as high or higher than in the other two marshes on the first sampling date, less

than 1 month after the 92Marsh was planted. Infaunal biomass in the 92Marsh was significantly lower than in the other marshes only during this first sampling period. Species richness within the infauna was generally low at all three marshes, which appears to be typical of these intertidal marsh habitats (Minello and Zimmerman 1992; Minello and Webb in review). However, there was little indication that the number of species present differed among the three marshes, except for the absence of crustaceans in the 92Marsh during the first sampling period.

The 92Marsh differed from the two older marshes in the abundance of dominant species and in the overall trophic structure within the polychaetes. These differences persisted throughout the two-year study period.

The similarities and differences among the three marshes indicate that many characteristics of infaunal populations in some created salt marshes develop rapidly and perhaps reach a developmental plateau within the first year. If other marsh characteristics such as elevation are comparable (Minello and Webb, in review), infaunal populations in these created marshes may also become similar to populations in natural marshes within

the first year. Differences in trophic structure and species assemblages may persist for longer periods.

The two most abundant organisms in these marshes, *Streblospio benedicti* and *Capitella capitata*, are common in shallow, soft bottom habitats of the Gulf of Mexico (Flint and Younk 1983; Ubelacker and Johnson 1984). Although both were found in all three marshes at Pelican Spit, their distribution among and within the marshes differed. *S. benedicti* was the dominant infaunal organism in the 83Marsh and 87Marsh, while *C. capitata* dominated the 92Marsh. In the inner marsh habitat, the density of *S. benedicti* was often significantly lower in the 92Marsh than in the other marshes. The density of *C. capitata*, was significantly higher in the 92Marsh than in the other marshes, and this difference was most pronounced in the inner marsh habitat.

Both *S. benedicti* and *C. capitata* are considered opportunists, and exhibit certain characteristics which may have contributed to the observed results of this study. An opportunistic species is one which exhibits 1) a lack of equilibrium population size, 2) a lack of density dependent mortality, 3) the ability to increase its population rapidly, 4) a high birth rate, 5) poor competitive ability, 6) good dispersal ability, and 7) a

high percentage of resources devoted to reproduction (Grassle and Grassle 1974). Based on time of appearance following a disturbance, rate of increase, and total mortality, Grassle and Grassle (1974) classified *C. capitata* as the most opportunistic species found in their study; *S. benedicti* ranked fifth. *C. capitata* has also been observed as the first species to occupy newly dredged material, reaching a population maximum four months after sediment was deposited (Reish 1962). Populations of these pioneer species can fluctuate greatly. The predominance of opportunists may have contributed to the rapid development of infauna in the new marsh.

Marsh Characteristics Which Affect Infaunal Abundance

Because infauna live, feed, and reproduce in close association with the marsh substrate, physical characteristics of the sediment can influence their numbers and distribution, and sediment grain size has been directly related to infaunal populations (Sanders 1958; Gilmore and Trent 1974; Whitlach 1977; Weston 1988; Ishikawa 1989; Jones et al. 1990; Jaramillo and McLachlan 1993; Yates et al. 1993; Long and Poiner 1994). Sediments in the three marshes consisted primarily of sand sized

particles.

High densities of surface deposit feeders, such as *S. benedicti*, are typical in sandy sediments (Flint and Kalke 1986; Gaston 1987) such as those found at Pelican Spit. However, neither total infaunal abundance, nor the abundance of these dominant species appeared to be correlated with sediment grain size. Folk (1980) suggests that other measures of sediment texture, such as grain shape and sediment compactness, can also influence infaunal populations. Although infaunal abundance was not correlated with sediment grain size, there was a relationship between grain size and the amount of organic matter in the sediments (SOC)(Table 3), with finer sediments containing more organic matter. Other studies have demonstrated relationships between sediment grain size, SOC, and infaunal abundance and distribution (Penas and Gonzales 1983; Gaston 1987; Riggs 1996). Taghon (1982) observed that some deposit feeders select food particles, based on size and organic coating.

Organic material in the sediment is potential food for infauna, and sediment organic content (SOC) has been cited as a major controlling factor for infaunal populations (Whitlach 1980; Butman and Grassle 1992). Two common findings in created marshes also suggest that

SOC may have an impact on infaunal abundances; created salt marshes support lower infaunal abundances than their natural counterparts (Cammen 1976 a,b; Moy and Levin 1991; Sacco et al. 1994) and contain lower levels of SOC than natural marshes (Shisler and Charrette 1984; Craft et al. 1988; Craft et al. 1991a; Langis et al. 1991; Moy and Levin 1991; Sacco et al. 1994).

Between-habitat species richness of both surface and subsurface deposit feeders has been correlated with the supply of food in sediments (Whitlach 1980). In addition, differences in SOC have also been discovered among created marshes of different ages (Osgood and Zieman 1993), indicating that SOC may be dependent upon marsh age. If there is a relationship between infauna and SOC, and SOC increases over time, then infaunal abundances in created marshes could be expected to increase over time. The feeding habits of the two most abundant species at Pelican Spit indicate that they may be affected by concentrations of organic matter in the sediment.

Streblospio can switch between suspension and surface deposit feeding modes (Gaston 1987), based on the flux of suspended particles (Taghon et al. 1980; Dauer 1983), and feeds on plankton, organic aggregates, and

sediment (Levin 1986). *S. benedicti* feeds selectively, and although it typically builds tubes, it is capable of leaving them (Fauchald and Jumars 1979). Nutrient enrichment has resulted in increased body size, as well as increased reproductive activity in *Streblospio* (Levin 1986).

Capitella is a subsurface deposit feeder, which ingests sediment and associated detritus and microflora (Gaston 1987). Although *C. capitata* is considered a non-selective feeder, Fauchald and Jumars (1979) discovered that guts of the specimens they examined always contained algae, suggesting that some selection is possible. *C. capitata* can build tubes at or near the surface, although it is normally considered a motile feeder (Fauchald and Jumars 1979). The reproductive output of *Capitella* is known to vary with food quantity and quality (Gremare et al. 1988), and it has been demonstrated that *Capitella* larvae selected for settlement sites containing organic matter over glass beads of the same size. In doing so, they select habitats consistent with the food requirements and observed distribution of adults in the field (Butman and Grassle 1992).

Despite evidence in the literature linking SOC to infaunal abundance, I found no significant positive

relationship between SOC and abundance of the infauna examined (Table 4). In fact, in some instances, there was a negative relationship between SOC and infaunal abundance. This negative relationship was apparently due to the high SOC values found along the inner transect of the 87Marsh in association with low infaunal abundances. The inner transect of the 87Marsh also had sediments with a high percentage of clay, and sediment grain size may have affected infaunal abundance. In addition, this area of the 87Marsh supported large numbers of nesting Forster's terns (*sterna forsteri*) and black skimmers (*Rynchops nigra*) compared with the other marshes, and brown pelicans (*Pelecanus occidentalis*) nested on the adjacent beach area. White pelicans (*Pelecanus erythrorhynchos*) and several unidentified members of the gull family (Laridae) were also present on the adjacent beach area. These birds may have enriched the organic content of the sediment with nest materials and waste products. The lack of a positive relationship between SOC and infaunal abundance, suggests that the infauna were not using SOC as an important food source, or that other factors control population size.

Other studies have failed to demonstrate a relationship between sediment organic content and

infaunal populations. In studies conducted in the Gulf of Carpentaria (Australia), Burford et al. (1994) found that when they controlled for variation due to sediment grain size, SOC was not correlated with infaunal abundance. By analyzing chlorophyll and carotenoid pigments which are the products of benthic microalgae, phytoplankton detritus, zooplankton fecal pellets, and infauna, Burford et al. (1994) examined the roles of microalgae and phytoplankton as an infaunal food source, and discovered correlations between infauna and these pigments which suggest that phytoplankton is a food source for infauna. Wiltse et al. (1984) found that adding urea fertilizer to predator exclusion cages in a salt marsh did not benefit deposit feeders, including *S. benedicti* and *C. capitata*. Their data indicated that in the absence of predators, food was not limiting in that habitat. Other nutrient enrichment studies have demonstrated that elevated concentrations of SOC may have temporary negative effects on infauna (Spies et al. 1988; Forbes and Lopez 1990).

Organic matter values were low in all three marshes, and were higher when measured by ashing than when measured by digestion. The relatively high SOC values obtained by ashing likely resulted from the

combustion of refractory material, which is not digested by the rapid oxidation technique (Pacific Estuarine Research Laboratory 1990). It is possible that we did not observe a relationship between infaunal populations and SOC levels in the marshes at Pelican Spit because there was so little organic matter in the sediments, and some of it was refractory.

There is some concern over the loss of pore water or $CaCO_3$ from sediments which are ashed at high temperatures or for long periods of time (Dean 1974; Mook and Hoskin 1982; Dankers and Laane 1983; Craft et al. 1991b), but the sediments at Pelican Spit contained very little shell material and also had a relatively low clay content. These characteristics, along with the fact that the sediments were ashed at a moderate temperature (100°C)for a moderate period of time (4 hours), minimize the risk of overestimating SOC using this method.

Detrital macroorganic matter (DMOM) is another food source potentially available to infauna, and is made up of the dead roots and rhizomes of *S.alterniflora*, as well as other detritus. Infauna are known to feed on detritus and its associated microflora (Cammen 1980; Reice and Stiven 1983; Stuart et al. 1985; Mann 1988). Detritus was present in the guts of all the capitellids examined

by Gaston in his 1987 study, and *Capitella* is also known to incorporate *Spartina* detritus (Tenore 1977 a, b; Tenore and Haines 1980).

Despite the abundance of deposit feeders in these marshes, there was no consistent relationship between DMOM and infaunal abundance in this study (Table 4). There was no positive relationship between total infaunal abundance and DMOM. In fact, there was a negative relationship between DMOM and infaunal abundance during the fall. The abundance of *C. capitata* was not related to DMOM during any of the four seasons. When regression analyses were repeated, using data for each of the marshes separately, positive correlations did exist between DMOM and the abundances of total infauna, *S. benedicti* and *C. capitata* in the 92Marsh. DMOM was lower in the 92Marsh than in the other marshes (Fig. 7). In the 83Marsh, *C. capitata* was the only organism affected by DMOM levels.

The lack of positive relationships between infaunal abundance and SOC or DMOM may indicate that organisms in these marshes derive their nutrition from a source other than those considered in this study, or that other factors control infaunal population size. The availability of detritus to deposit feeders changes with

decomposition, and decomposition rates differ, depending on the source of the detritus and the proportion of nutrients to refractory material (Tenore 1975; 1977 a, b; Tenore and Haines 1980). *Spartina* decays slowly and has a lower utilization rate than other sources (Tenore and Haines 1980) such as benthic algae. Findlay and Tenore (1982) suggested that much of *Capitella*'s nitrogen is supplied through the digestion of algae.

Salt marshes are characterized by the growth of intertidal macrophytes, and above-ground growth of *S. alterniflora* is rapid in created salt marshes (Burger and Shisler 1983; Seneca et al. 1985; Broome et al. 1986; LaSalle et al. 1991). However, above-ground plant characteristics are not correlated with infaunal abundances (Cammen 1976a; Moy and Levin 1991; Minello and Zimmerman 1992). Below-ground biomass, especially live roots and rhizomes (LMOM), are correlated with the abundances of a variety of infauna (Osenga and Coull 1983; Minello and Zimmerman 1992).

Infaunal abundances in the marshes considered in this study were frequently related to the amount of live roots and rhizomes (LMOM) present (Table 4). Of the three independent variables considered, LMOM occurred most often in the regression models, and there were

positive relationships between LMOM and abundances of total infauna, crustaceans and *S. benedicti*. In addition, the relationship with LMOM was seen in all three marshes, despite the fact that LMOM levels were significantly lower in the new marsh (Fig. 7). The significance of LMOM levels in all three marshes may indicate that some benefit is supplied by the presence of LMOM, which may be limiting in these marshes.

The relationship between LMOM and infaunal abundance may also be an effect of proximity to *S. alterniflora* culms. In this study, cores taken at *S. alterniflora* culms included more LMOM. There were also more infauna, especially crustaceans, collected near stems (Fig. 11). The most abundant crustacean was the amphipod, *Gammarus mucronatus* (Table 1).

There are several possible explanations for the relationships with LMOM. *Spartina* roots and rhizomes are closely tied to activities of denitrifying organisms in the soil (Sherr and Payne 1978), and may provide additional food for deposit feeders. *Spartina* roots may also produce micro-oxygenated zones within the soil which increase the amount of oxygenated sediment available to infauna (Teal and Kanwisher 1966; Armstrong 1979; Mendelssohn and Postek 1982; Osenga and Coull 1983;

LaSalle et al. 1991). In addition, the structural complexity of the roots and rhizomes of *Spartina* may provide refuge from predation by nekton (LaSalle and Rozas 1991).

Infauna in these marshes reach peak abundance in early spring and decline to lowest levels during summer (Fig. 3). Predation pressure from nekton is lowest in winter (Zimmerman et al. 1991). Although predator densities are high during the other three seasons, accessibility of the marsh surface is somewhat lower during the summer, due to shorter periods of marsh inundation. LMOM is positively correlated with infaunal abundance during spring, summer and fall, and this relationship is strongest during spring and fall, when high densities of predators have access to the marsh surface. In addition, the relationship between LMOM and infauna was strongest in marsh edge habitat, where predation pressure by nekton is highest (Baltz et al. 1993; Minello et al. 1994; Peterson and Turner 1994). The occurrence of a relationship between LMOM and infauna under conditions of higher predation pressure suggests that LMOM may reduce predation pressure on the infauna.

The lack of strong relationships between infaunal abundance and SOC, DMOM, and LMOM in my data suggests

that other environmental factors may be important in determining population size for infauna. A variety of biological interactions, including density-dependent effects, such as adult-recruit interactions (Kent and Day 1983), interspecific and intraspecific competition (Peterson 1977; Wiens 1977; DeWitt 1987; Kristensen 1988; Taghon 1992), and larval settlement characteristics (Rodriguez at al 1993), may also regulate infaunal populations. Although the dominant species in the Pelican Spit marshes are generally considered poor competitors, they are capable of proliferating quickly (Grassle and Grassle 1974). *S. benedicti* can switch between planktotrophic and lecithotrophic reproduction (Levin 1984 a, b). *C. capitata* is capable of year round reproduction and of producing planktonic or benthic larvae (Grassle and Grassle 1974). These characteristics contribute to the rapid colonization and population growth observed for these animals.

Physical factors, such as salinity (Flint and Younk 1983; Dauer et al. 1987; Jones et al. 1990), dissolved oxygen (Dauer et al. 1992), photoperiod (Chu and Levin 1989), and temperature (Chu and Levin 1989) have all been determined to influence infaunal populations. Because of the close proximity of the three marshes at Pelican Spit,

however, these physical factors should be similar among marshes. Disturbance has also been shown to influence infaunal populations (Flint and Younk 1983).

Disturbance as one possible explanation for the similarities in infaunal abundance, biomass, and species richness among the three marshes should be addressed. Open-water disposal of dredged material is not a well-controlled operation. Depositing new sediment to create the 92Marsh may have impacted the older marshes on Pelican Spit, essentially causing these marshes to revert back to some earlier developmental stage. At the initiation of sampling in July 1992, I selected areas in the two older marshes that did not appear to have new sediment deposition, however, I can not be certain that sediment resuspended from the disposal area was not deposited on these marshes throughout the study period. Comparison of the 83Marsh and 87Marsh during the study with these same marshes in 1990/1991, however, does not appear to support this alternate disturbance hypothesis. If the surface sediments were replaced in the 83Marsh and 87Marsh due to the creation of the 92Marsh, I would expect reduced MOM after the marsh creation.

Development Over Time

In less than one year, the 92Marsh became similar to the two older marshes on the basis of total infaunal density, biomass, and species richness. Cammen (1976b) listed five factors affecting the development time of infauna in created marshes. These factors include similarity of elevation, sediment particle size, and sedimentation rates of the marshes, as well as proximity to natural marshes and potential colonists and maturity of the natural target marsh community. At Pelican Spit, the 92Marsh had similar sediment properties to the two established marshes. This newly-created marsh had a shallower slope than the 83Marsh and 87Marsh, but the same elevations were sampled in each marsh. All three marshes were the same distance from the nearest natural marsh, which I did not examine as part of this study. The 83Marsh and 87Marsh were the likely source of colonists for the newly established marsh. Past studies suggest that the trophic structure in the natural marshes appears similar to the two older created marshes, but not to the 92Marsh (Minello and Webb, in review).

Other studies indicate that organic matter in created salt marshes increases over time (Friedman and Dewitt 1978; Lindau and Hossner 1981; Craft et al. 1988;

LaSalle et al. 1991). Although MOM has been estimated to reach natural marsh levels in 15-30 years, accumulation of N, P, and SOC may take longer (Craft et al. 1988). Sacco et al. (1994) found that created marshes between 1 and 17 years of age still had lower SOC than natural ones. At Pelican Spit, there was no evidence of any increase over time in SOC or MOM, either through a comparison between the newest and oldest marshes, or over the two year study period. It is possible that I did not observe increases because all three marshes were relatively young. It appears that factors other than age are influencing the development of these marshes.

CONCLUSIONS

In such a complex and dynamic environment, it is difficult to determine which of the many potential factors control the development of infaunal populations in created salt marshes. The newly planted marsh at Pelican Spit quickly resembled the 5 and 9 year old marshes on the basis of infaunal abundance and biomass, and species richness. Differences in trophic structure and dominant species persisted over the two-year study period. Macroorganic matter and sediment organic matter were lowest in the newly planted marsh. Over the two-year study period, macroorganic matter did increase slightly in the 92Marsh. SOC was low in all three marshes, and there was no positive relationship between infaunal abundance and SOC. There was a positive relationship between live macroorganic matter and infaunal abundance.

LITERATURE CITED

ARMSTRONG, W. 1979. Aeration in higher plants. *Advanced Botanical Research* 7:225-332.

BALTZ, D. M., C. RAKOCINSKI, and J. W. FLEEGER. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environmental Biology of Fishes* 36:109-126.

BELL, S. S. and B. C. COULL. 1978. Field evidence that shrimp predation regulates meiofauna. *Oecologia* 35:141-148.

BROOME, S. W., E. D. SENECA, and W. W. WOODHOUSE. 1986. Long-term growth and development of transplants of the salt-marsh grass *Spartina alterniflora*. *Estuaries* 9:63-74.

BROOME, S. W., E. D. SENECA, and W. W. WOODHOUSE. 1988. Tidal salt marsh restoration. *Aquatic Botany* 32:1-22.

BURFORD, M. A., B. G. LONG, and P. C. ROTHLISBERG. 1994. Sedimentary pigments and organic carbon in relation to microalgal and benthic faunal abundance in the Gulf of Carpentaria. *Marine Ecology Progress Series* 103:111-117.

BURGER, J. and J. SHISLER. 1983. Succession and productivity on perturbed and natural Spartina salt-marsh areas in New Jersey. *Estuaries* 6:50-56.

BUTMAN, C. A. and J. P. GRASSLE. 1992. Active habitat selection by *Capitella sp-1* larvae. 1. 2-Choice experiments in still water and flume flows. *Journal of Marine Research* 50:669-715.

CAMMEN, L. M. 1976a. Abundance and production of macroinvertebrates from natural and artificially established salt marshes in North Carolina. *American Midland Naturalist* 96:487-493.

CAMMEN, L. M. 1976b. Macroinvertebrate colonization of *Spartina* marshes artificially established on dredge spoil. *Estuarine, Coastal and Marine Science* 4:357-372.

CAMMEN, L. M. 1980. The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. *Marine Biology* 61:9-20.

CHU, J.-W. and L. A. LEVIN. 1989. Photoperiod and temperature regulation of growth and reproduction in *Streblospio benedicti* (Polychaeta: Spionidae). *Invertebrate Reproduction and Development* 15:131-142.

CRAFT, C. B., S. W. BROOME, and E. D. SENECA. 1988. Nitrogen, phosphorus and organic carbon pools in natural and transplanted marsh soils. *Estuaries* 11:272-280.

CRAFT, C. B., E. D. SENECA, and S. W. BROOME. 1991a. Porewater chemistry of natural and created marsh soils. *Journal of Experimental Marine Biology and Ecology* 152:187-200.

CRAFT, C. B., E. D. SENECA, and S. W. BROOME. 1991b. Loss on ignition and Kjeldahl digestion for estimating organic carbon and total nitrogen in estuarine marsh soils: Calibration with dry combustion. *Estuaries* 14:175-179.

DANKERS, N. and R. LAANE. 1983. A comparison of wet oxidation and loss on ignition of organic material in suspended matter. *Environmental Technology Letters* 4:283-290.

DAUER, D. M. 1983. Functional morphology and feeding behavior of *Scolelepis squamata* (Polychaeta: Spionidae). *Marine Biology* 77:279-285.

DAUER, D. M., R. M. EWING, and A. J. RODI. 1987. Macrobenthic distribution within the sediment along an estuarine salinity gradient - benthic studies of the lower Chesapeake Bay. *Internationale Revue Der Gesamten Hydrobiologie* 72:529-538.

DAUER, D. M., A. J. RODI, and J. A. RANASINGHE. 1992. Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. *Estuaries* 15:384-391.

DEAN, W. E. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss of ignition: Comparison with other methods. *Journal of Sedimentary Petrology* 44:242-248.

DEWITT, T. H. 1987. Microhabitat selection and colonization rates of a benthic amphipod. *Marine Ecology Progress Series* 36:237-250.

FAUCHALD, K. and P. A. JUMARS. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology* Annual Review 17:193-284.

FINDLAY, S. and K. R. TENORE. 1982. Nitrogen source for a detritivore: Detritus substrate versus associated microbes. *Science* 218:371-373.

FLINT, R. W. and R. D. KALKE. 1986. Biological enhancement of estuarine benthic community structure. *Marine Ecology Progress Series* 31:23-33.

FLINT, R. W. and J. A. YOUNK. 1983. Estuarine benthos: Long-term community structure variations, Corpus Christi Bay, Texas. *Estuaries* 6:126-141.

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